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Austral Hepaticae. 32. A Revision of the Genus *Lepidozia* (Hepaticae) for New Zealand

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Abstract

Twenty-two species of *Lepidozia* are recognized in New Zealand, and these are placed in five subgenera. The following new taxa are proposed: *Lepidozia* subg. *Notholepidozia* Schust., *L. acantha* Engel, *L. bidens* Engel, *L. elobata* Schust., *L. fugax* Engel, *L. glaucescens* Engel, *L. laevifolia* (Hook. f. & Tayl.) G. L. & N. var. *acutiloba* Engel, *L. laevifolia* var. *alpina* Schust. & Engel, *L. novae-zelandiae* Steph. var. *heterostipa* Schust., *L. novae-zelandiae* var. *minima* Schust., *L. obtusiloba* Steph. var. *parvula* Engel, *L. ornata* Engel and *L. pumila* Engel.

A key to the *Lepidozia* species in New Zealand is included.

Introduction

The genus *Lepidozia* was proposed by Dumortier in 1835 (p. 19), based on an earlier taxon, *Pleuroschisma* sect. *Lepidozia* (Dumortier, 1831, p. 69). Basically, the latter concept included taxa now placed into *Bazzania* and allies (the *Pleuroschisma* element) and a series of eight taxa that constitute *Lepidozia.* In subsequent years a wide range of other taxa were assigned to *Lepidozia* but failed to fit into the genus as we here define it. Spruce (1885, p. 358–360) divided the genus into two subgenera, *Eu-Lepidozia* (= *Lepidozia s. str.*) and *Micro-Lepidozia.* The latter was divided into two unnamed groups with four species, of which the first three constitute *Microlepidozia s. str.,* today placed within *Kurzia.* v. Mart. The fourth species (*L. chaetophylla* Spruce) represents the autonomous genus *Telaranea.*

In the 19th century and into the early years of the 20th century, various taxa, such as the southern South American *L. oligophylla* and the temperate Australasian *L. capilligera* (cf. Gottsche et al., 1845, pp. 201, 204), were included under "*Lepidozia.*" These taxa were segregated from *Lepidozia* by Fulford and Taylor (1959) as *Neolepidozia,* with *Lepidozia* (*Jungermannia*) *capilligera* as the type. Taxa falling into this last element were regarded (Schuster, 1963, 1969) as constituting a subgenus of *Telaranea.* Finally, an isolated element, *Lepidozia integristipula* Steph. (Stephani, 1922, p. 331), was segregated by Hodgson (1962b) and placed into the autonomous genus *Drucella.* Thus, at various times, taxa that today fit into *Bazzania, Telaranea* (incl. *Neolepidozia*), *Kurzia* (incl. as a subgenus of *Microlepidozia*), and *Drucella* were assigned to *Lepidozia.*

This confusion continued into the relatively recent account of the New Zealand species of the genus *Lepidozia* by Hodgson (1956). To date, this is the only revision of the New Zealand taxa. Hodgson assigned some 33 species to the genus, but of these 33 species, 22 presently belong to other genera (Table 1).

Thus, in the only prior revision of the New Zealand taxa of *Lepidozia,* the 33 species assigned to that genus belong in some five genera. Hodgson (1964, p. 70) assigned *Telaranea herzogii* to a sixth genus, *Arachniopsis,* which does not occur in New Zealand. Hodgson (1962) also segregated *Lepidozia glaucophylla,* which she had assigned in 1956 to *Lepidozia s. str.* (her subg. *Lepidozia*), to a new genus, *Lepidoziopsis;* this was transferred (Schuster, 1973) to *Lepidozia* subg. *Glaucolepidozia.*

From this brief account, it is evident that the New Zealand taxa of *Lepidozia* have been widely confused with other genera. Rather than 11 spe-

TABLE 1. Species assigned to the genus *Lepidozia* by Hodgson (1956).

Species name	Current disposition	Selected references
L. kirkii	retained in genus	this treatment
L. ulothrix	retained in genus	this treatmant
L. glaucophylla	retained in genus	this treatment
L. setigera	retained in genus	this treatment
L. laevifolia	retained in genus	this treatment
L. microphylla	retained in genus	this treatment
L. procera	retained in genus	this treatment
L. obtusiloba	retained in genus	this treatment
L. concinna	retained in genus	this treatment
L. pendulina	retained in genus	this treatment
L. integristipula	≡ *Drucella i.*	Hodgson (1962b); Schuster (1980)
L. martinii	≡ *Telaranea m.*	Schuster (1963)
L. dispar	= *Kurzia hippuroides*	Engel and Merrill (1996b)
L. remotifolia	≡ *Telaranea r.*	Hodgson (1962a)
L. tetradactyla	≡ *Telaranea t.*	Hodgson (1962a)
L. centipes	≡ *Telaranea c.*	Schuster (1963)
L. roseana	≡ *Telaranea tetrapila* var. *r.*	Engel and Merrill (1996a)
L. corticola	≡ *Telaranea c.*	Hodgson (1962a)
L. leptodictyon	= *Pseudocephalozia lepidozioides*	Engel and Schuster (1988)
L. patentissima	≡ *Telaranea p.*	Hodgson (1962a)
L. gottscheana	≡ *Telaranea g.*	Hodgson (1962a)
L. meridiana	≡ *Telaranea m.*	Hodgson (1962a)
L. spinosissima	retained in genus	this treatment
L. gibbsiana	≡ *Telaranea g.*	Hodgson (1965)
L. praenitens	≡ *Telaranea p.*	Hodgson (1962a)
L. radiata	belongs within *Telaranea* subg. *Tricholepidozia*	Schuster (1963)
L. pulcherrima	belongs within *Telaranea* subg. *Tricholepidozia*	Schuster (1963)
L. hippuroides	≡ *Kurzia h.*	Grolle (1964); Engel and Merrill (1996b)
L. compacta	≡ *Kurzia c.*	Grolle (1964); Schuster (1980)
L. allisonii	= *Kurzia hippuroides*	Grolle (1964); Engel and Merrill (1996b)
L. calcarata	≡ *Kurzia c.*	Grolle (1964); Schuster (1980)
L. herzogii	≡ *Telaranea h.*	Hodgson (1962a)
L. longiscypha	≡ *Paracromastigum l.*	Grolle (1964, p. 177); Schuter and Engel (1996)

cies of "true" *Lepidozia,* as in Hodgson (1956), we now recognize some 22 species, of which seven are newly described here. The genus *s. str.* is thus a large and complex group in New Zealand, and a definition of *Lepidozia s. str.* emerges from the following conspectus. In the past, *Lepidozia* was confused chiefly with *Telaranea* subg. *Neolepidozia;* this problem is addressed under Affinities and Intrageneric Classification (p. 5).

After exclusion of the foreign elements, the genus remains forbiddingly complex, even after the exclusion of the more isolated elements. Taxonomic problems in the genus *s. str.* are discussed on pp. 5–8.

Conspectus of Generic and Subgeneric Elements Previously Confused with *Lepidozia*

1. Vegetative branches all or mostly *Frullania* type, lateral-terminal and/or ventral-intercalary (exc. *Pseudocephalozia*); stem with several to many cortical cells intervening between successive lateral leaves; oil-bodies present (vestigial or lacking from most cells in some *Kurzia* spp.) 2
   2. Leaves clearly incubous to transversely inserted; underleaves never present (vestigial in some *Telaranea* spp.); terminal branches abundant and lateral-intercalary leafy branches usually lacking 3
      3. Terminal branches of the *Microlepidozia* type (replacing dorsal half of lateral leaf) lacking, the lateral branches all *Frullania* type (replacing ventral half of a lateral leaf); oil-bodies present in all leaf cells, conspicuous, granular to botryoidal (exc. *L. reptans*); leaves ± incubously inserted; plants usually whitish or light to clear green, rarely brownish 4
         4. Stem without a conspicuous hyaloderm, the cortex firm- to thick-walled, the cells not conspicuously enlarged in diameter, mostly in numerous (>24) rows; leaf cells almost always firm, mostly thick-walled, usually relatively small in proportion to leaf, never tiered within the lamina; spores (as far as known) with granular exine; ♀ bracts usually shallowly lobed or lobulate . . . *Lepidozia* (Dum.) Dum.
         4. Stem with a conspicuous hyaloderm (exc. *Telaranea* subg. *Tricholepidozia*), formed of very large, soft-textured, leptodermous cells, the cortex of a limited number of cells (except *Telaranea* subg. *Tricholepidozia*), usually in 6–24 rows; leaf cells thin-walled, usually ± pellucid, large in proportion to leaf, ± tiered within lamina (or lamina lacking); spores delicately areolate; ♀ bracts very deeply (mostly 4-) lobed . . . . . *Telaranea* Spruce *ex* Schiffn.
      3. Terminal branches of both the *Microlepidozia* and *Frullania* types; oil-bodies of some or most leaf cells lacking or few (1–2, rarely 3–5) and homogeneous to few-segmented, less often granular; leaves usually transversely inserted (very deeply 3–4(5–6)-lobed); plants usually ± fuscous (exc. *Leucolepidozia,* which is nitid and whitish green). Stem with ± firm-walled cortical cells, usually in (8)9–14 rows (exc. subg. *Dendrolepidozia*) . . . . . *Kurzia* v. Mart.
   2. Leaves somewhat to clearly succubously inserted, only the dorsal end of the insertion line transverse; underleaves vestigial, a few isodiametric basal cells giving rise to 2–4 lobes formed of 1(2) fingerlike cells, each ending in a slime papilla; terminal branches rare or lacking in most phases, but with lateral-intercalary branches frequent. Leaves soft-textured and mostly 4-lobed . . . . . *Pseudocephalozia* Schust.[1]
1. Vegetative leafy branches thecal, lateral-intercalary (from axils of the incubous, asymmetrically 3-lobed lateral leaves); stem with 1–2 rows of strongly elongated, sublinear cortical cells intervening between successive lateral leaves; oil-bodies lacking (numerous lipid droplets may be present) . . . . . *Drucella* Hodgs.[2]
   [*D. integristipula* (Steph.) Hodgs.]

Of the five genera in the preceding conspectus, genera 1–3 belong in the subfamily Lepidozioideae (*sensu* Schuster, 1973, 1984), while genus 4, *Pseudocephalozia,* is an enigmatic genus that probably falls close to the point of origin of the Zoopsidoideae, a subfamily unusual in the Lepi-

[1] *Lepidozia leptodictyon* Herz. (*Trans. Roy. Soc. New Zealand* 68: 45. 1938) is placed as a synonym of *Pseudocephalozia lepidozioides* Schust. by Engel and Schuster (1988). *Pseudocephalozia lepidozioides* is treated in detail in Schuster and Engel (1974, p. 677, figs. 5–7).

[2] For this genus, see Schuster (1980, p. 411, figs. 17–18) and Boesen (1982).

doziaceae in developing succubous to longitudinally inserted leaves, although possibly also bearing "distant affinities to the Lembidoideae Schust." (cf. Schuster & Engel, 1974). The last genus, *Drucella,* is so isolated that it is split from other Lepidozioideae by Boesen (1982) as a tribe *Drucelleae* Boesen, elevated by Schuster (1984) to the status of an autonomous subfamily, the Drucelloideae (Boesen) Schust. After removal of these two last genera, a complex remains formed by *Lepidozia, Telaranea,* and *Kurzia.* These genera are clearly allied, but *Kurzia* seems to us to bear relatively remote affinities to the other two genera. It is distinct in (a) retaining the capacity to form *Microlepidozia*-type terminal branches; (b) a tendency for most taxa to lose oil-bodies from all or most leaf cells; (c) the transverse leaves, ranging in some taxa to clearly succubously inserted and oriented.

Lepidozia and *Telaranea,* however, are so closely allied that until relatively recently they were considered identical, or at least the *Neolepidozia* element was placed as a group "Symmetricae" in *Lepidozia,* while the subg. *Telaranea* element was recogized as an autonomous genus. The present segregation into two genera, with the "Symmetricae" element placed within *Telaranea,* was introduced in Schuster (1963).

Lepidozia (Dum.) Dum.

Pleuroschisma sect. *Lepidozia* Dum., Syll. Jungerm. Eur. Indig. 69. 1831.
Lepidozia (Dum.) Dum., Receuil Observ. Jungerm. 19. 1835, *nom. cons.*
Herpetium sect. *Lepidozia* Nees, Naturg. Eur. Leberm. 3: 31. 1838.
Lepidoziopsis Hodgs., Rec. Domin. Mus. 4: 105. 1962.

Plants anisophyllous, creeping to loosely prostrate to, more often, somewhat ascending, rarely stiffly erect, the leafy shoots mostly loosely attached to substrate, firm, yellowish or whitish to olive-green, rarely brownish in life, rarely glaucous, usually relatively opaque and chlorophyllose, vigorous to medium-sized, usually 0.5–2.5(4) mm wide. Branching irregular to regular, copiously 1- to 2- or 2–3-pinnate, of *Frullania* type; *Acromastigum* type present in *Dendrolepidozia* and one species of sect. *Notholepidozia; Microlepidozia*-type branches and lateral-intercalary branches lacking; ventral-intercalary microphyllous or leafy branches in some taxa; lower lateral terminal branches partly or mostly attenuate at the apices, often becoming rhizoid-bearing; half-leaf associated with *Frullania*-type branches usually bifid; initial branch underleaf of primary branches usually bifid, less often unlobed or trifid to quadrifid. Stem firm to rigid, terete to elliptical in cross section, with (18)20–32 or more rows of firm-walled cortical cells, typically little or at most moderately larger in diameter than those of adjoining medulla, not forming a discrete hyaloderm;[3] subepidermal layers occasionally present, composed of thick-walled cells; medullary cells equal to or slightly smaller than cortical, firm-walled (the outer sometimes strongly so). Rhizoids of normal-leaved axes usually rare or absent, except at shoot bases, arising from underleaf bases; rhizoids on flagelliform shoots or shoot apices from all three merophyte rows. Leaves almost without exception 4-lobed or 4-lobulate on main axes, incubous to subtransverse, the insertion extending to stem midline dorsally, the leaves typically asymmetrical, the dorsal half (and dorsal 1–2 lobes) larger than the ventral, the lobes usually many-celled (at bases 3–4 or more cells broad in most taxa), the cells similar to those of lamina, the lobes usually sharp, often deflexed or inflexed in most taxa; lamina margins entire or toothed to spinose-dentate or ciliate. Cells not tiered within the lamina, firm-walled, the lumina often guttulate or rounded, the trigones concave-sided and mostly obscurely defined; median cells mostly 18–25(40) μm wide in median portions of lamina, cuticle smooth or clearly papillose. Oil-bodies present in all leaf cells, colorless, usually (2)5–16 per cell, relatively large, usually granular-botryoidal, less often subhomogeneous. No asexual reproduction[4] or (*L. fugax,* occas. in *L. digitata*) reproduction via fragmenting or caducous leaf lobes. Underleaves usually 0.5 or less the lateral leaves in area, transversely inserted, symmetrically 4-lobed on main axes.

Dio- or rarely (*L. reptans*) autoecious. Gametangial branches all short (♂ rarely ± elongated, leafy), devoid of normal leaves and underleaves, ventral-intercalary in origin (the androecia less

[3] Some taxa, such as *L. microphylla,* have two or more strata of smaller cells lying within a rather distinct hyaloderm (Fig. 9 : 14). Even though stem anatomy, in general, serves to separate *Lepidozia* from *Telaranea,* the distinction is bridged by several exceptions.

[4] Degenkolbe (1938, p. 87) reported gemmae in the generic type, *L. reptans* (L.) Dum. Over four decades of study of masses of material of this species have not revealed any gemmiparous population of this or any other true *Lepidozia* species.

frequently terminal on primary and secondary branches). Androecia typically spicate, smaller than vegetative shoots, the bracts concave, ± imbricate, lobed like (but usually more shallowly than) vegetative leaves; antheridia 1–2 per bract, the stalk 2-seriate; bracteoles small, lacking antheridia. ♀ Branches with several progressively larger gyres of identical bracts + bracteoles, the inner 1–2 gyres of bracts + bracteoles erect, concave, clearly sheathing the perianth, the innermost bracts mostly oval or ellipsoidal in outline, 4(6)-lobed to lobulate at the apex, but occasionally bracts 2–4 dentate-lobulate. Perianth fusiform or ellipsoidal-fusiform, bluntly 3-gonous in at least the narrowed distal sectors, the mouth usually crenulate to crenate-denticulate.

Seta with (8)12–16 large epidermal + 16 or more rows of much smaller internal cells. Capsule ellipsoidal to oblong, the wall 3–5(6)-layered (in studied taxa); epidermal cells with ± oblong cells, often imperfectly tiered, the primary longitudinal and all transverse walls normally lacking pigmented thickenings, the secondary (longitudinal) walls with conspicuous radial (nodular) thickenings, often ± coalescent; inner cells narrower, narrowly oblong, with radial (nodular) thickenings, ± connected by weak, often vestigial, tangential bands. Spores papillose-vermiculate, less than 1.5× the diameter of the 2-spiral elaters.

TYPE—*Lepidozia reptans* (L.) Dum. (The type species is unfortunately not representative of the genus; cf. remarks under subgenus *Notholepidozia,* p. 31.)

Lepidozia is a large, taxonomically complex genus that is found in almost all areas except the Arctic and true Antarctic regions, arid continental regions, and some isolated lowland islands. Although Stephani (1922) included some 297 taxa in the genus, and a few have been described subsequently, many of the taxa he referred here have now been assigned to other genera (*Telaranea,* incl. *Neolepidozia; Kurzia,* incl. *Microlepidozia; Drucella*). Even after exclusion of these elements, the genus remains large and unwieldy, although many described taxa are synonyms. On that account, the genus was divided into five subgenera in Schuster (1973, pp. 385–388); two other subgenera, *Notholepidozia* Schust. and *Austrolepidozia* Schust., are accepted here. Of these six subgenera, only *Chaetolepidozia* Schust. and *Cladolepidozia* Schust. do not occur regionally.

The center of diversity of the genus is the region of former Gondwanaland: present-day South America (with 30 species recognized by Fulford, 1966), New Zealand (we recognize 22 species), ranging to New Caledonia, New Guinea, and the Indomalayan region. Africa is much poorer in species.[5] By contrast, Holarctic regions bear only an impoverished representation of species: All of eastern North America has a single species (*L. reptans*), and Europe has only three species (*L. cupressina* (Sw.) Lindenb., *L. pearsonii* Spruce, and *L. reptans*). The holarctic taxa belong to the single subgenus *Lepidozia.* By contrast, in New Zealand we find representatives of five of the seven subgenera, while the other two subgenera occur in New Guinea (largely Gondwanalandic in origin) westward into Indomalaya.

Affinities and Intrageneric Classification

As the conspectus clearly suggests, *Lepidozia* is most immediately allied to *Telaranea.* In addition to the critera in the conspectus, a series of additional features and, more important, a suite of phylogenetically relevant "tendencies" separate the two genera. A discussion of these follows.

1. Leaf lobe number is relatively stable in *Lepidozia,* with main axes usually with 4-lobed leaves, although sporadic 3- and 5-lobed leaves occasionally occur in some taxa; in *Telaranea,* rampant variation from 2- to 3–4- to 5–6- or even 8–13-lobed leaves occurs (Figs. 1 : 1–6; 2 : 1–3; 3 : 1, 2; 5 : 6, 7).

2. The leaf tends to be conspicuously asymmetrical in *Lepidozia,* with a longer dorsal lobe (and margin) than ventral lobe (and margin; Figs. 9 : 3; 10 : 3, 4), while in *Telaranea* the leaves are typically symmetrical or almost so (Fig. 5 : 5–7). However, obvious exceptions occur; thus, in *T. inaequalis* Schust., the bifid leaves have a conspicuously shorter ventral lobe (cf. Schuster, 1969, fig. 88 : 5), and in the very different *T. mooreana* (Steph.) Schust., the dorsal portion of the disc tends to be higher than the ventral (Fig. 2 : 3); the same is true of such typical taxa of *Telaranea* subg. *Neolepidozia* as *T. remotifolia* (Hodgs.) Hodgs., in which the leaf shape is decidedly *Lepidozia*-like (cf. Fig. 1 : 1–6).

[5] However, the closely allied genus *Sprucella* Steph., with two endemic species, occurs in tropical Africa. This is so closely allied to *Lepidozia* that some workers include the two species within *Lepidozia.* It differs from *Lepidozia s. str.* in the 2–3-lobed lateral leaves, strongly reduced underleaves, and the leaf areolation (cf. Schuster, 2000).

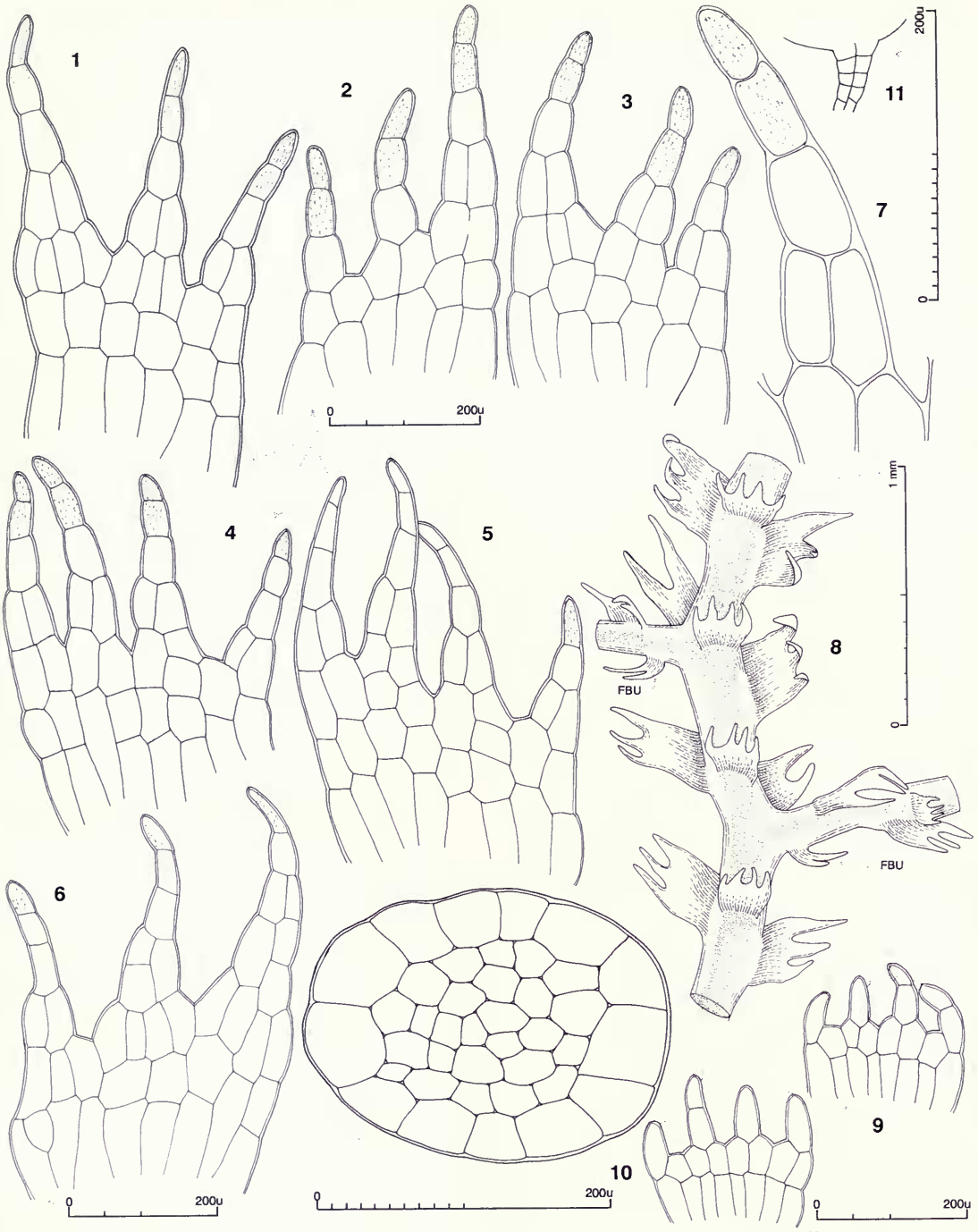

FIG. 1. *Telaranea remotifolia* Hodgs. **1–6.** Leaves, cellular detail. **7.** Dorsal lobe of leaf. **8.** Main shoot (fbu = first branch underleaf), medullary strand shown with stipple; ventral view. **9.** Underleaves, cellular detail. **10.** Stem, cross section. **11.** Antheridial stalk. **12, 13.** First branch underleaves (both at same scale). (Figs. 1, 5–6, 10, 12, 13 from *Engel 18921,* New Zealand, South Is., Otago Prov., Mt. Aspiring Natl. Park, Blue River; 2–4, 7–9 from type; 11 from *Child 5366,* New Zealand, South Is., Westland Prov., 5 km N of Runanga.)

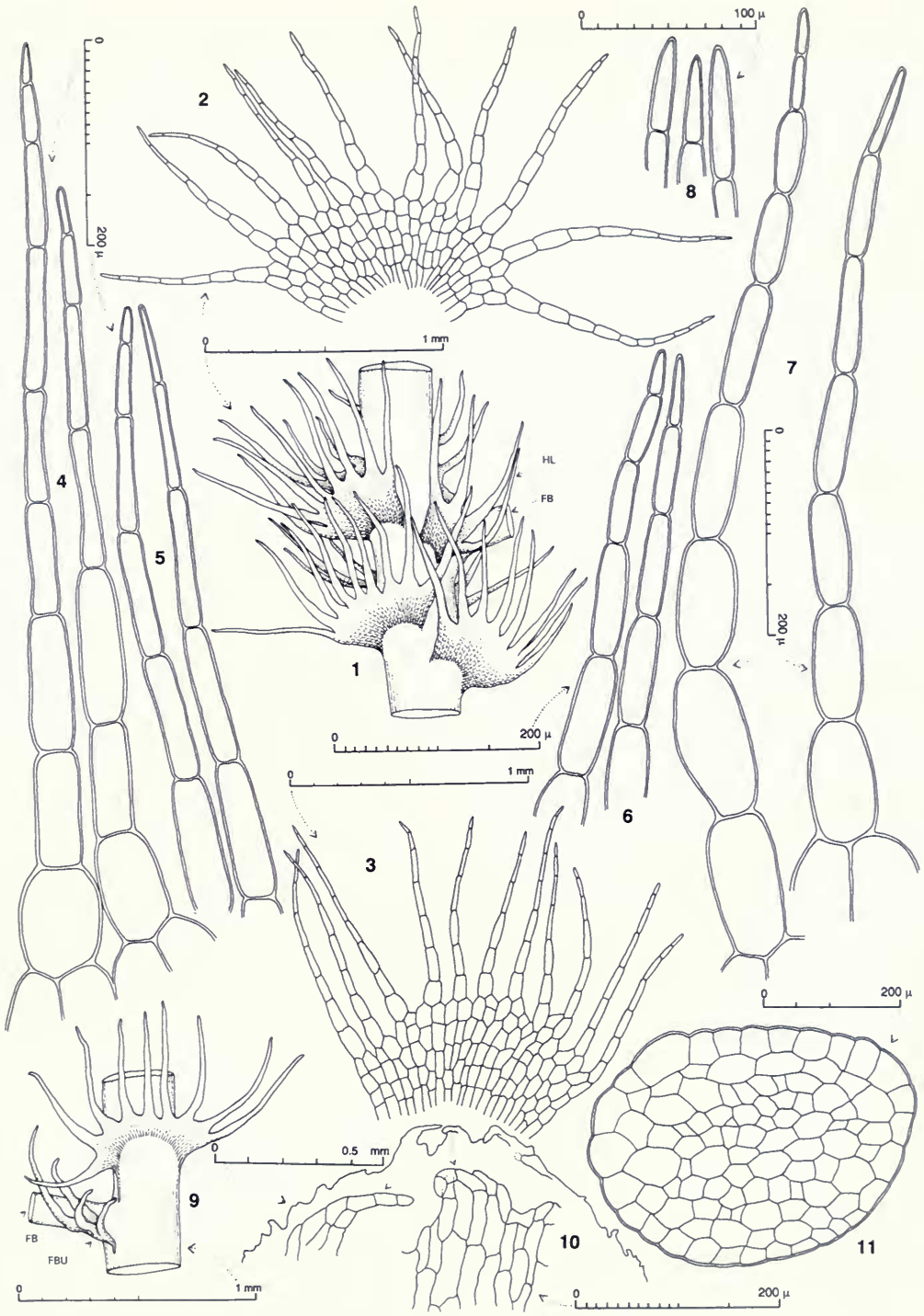

FIG. 2. *Telaranea mooreana* (Steph.) Schust. **1.** Sector of main shoot, dorsal view (FB = *Frullania*-type branch; HL = half-leaf). **2, 3.** Leaves. **4–7.** Leaf lobes. **8.** Terminal cells of leaf lobes. **9.** Sector of main shoot, ventral view (FB = *Frullania*-type branch; FBU = first branch underleaf). **10.** Apex of innermost ♀ bract, with (at arrows) 2 lobules shown in detail. **11.** Stem, cross section. (Figs. 1, 6, 9 from *Engel 21771,* New Zealand, South Is., Westland Prov., ca. 4 km N of Haast River; 2, 7 from type of *Lepidozia pulcherrima*; 3, 4, 8 from type of *Lepidozia mooreana*; 10, 11 from *Engel 16407,* Tasmania, road between Zeehan and Trial Harbour; 5 from *Engel 19927*, Tasmania, Tahune Forest Reserve, along Huon River.)

3. The stem in *Lepidozia* generally lacks obvious differentiation of a hyaloderm (Figs. 8 : 9; 9 : 14), although cortical cells in some taxa, including the generic type, tend to be somewhat larger than the medullary (cf. fig. 85 : 8 in Schuster, l.c., and Fig. 6 : 13 in this paper). In many taxa the cortical cells and/or several strata of intracortical cells may be strikingly thick-walled, as in *L. spinosissima* and *L. microphylla* (Figs. 8 : 7, 9; 9 : 14), and stems are quite rigid. In general, cortical cells are at least slightly firm-walled.[6] In *Telaranea,* in contrast, at least dorsal and dorsolateral cortical cells are much larger than medullary cells (Figs. 1 : 10; 5 : 4), even though this is hardly distinct in subg. *Tricholepidozia* (Fig. 2 : 11 of *T. mooreana*). In *Telaranea* there is never a clearly defined zone of thick-walled cells lying within the hyaloderm (Figs. 2 : 11; 5 : 4), whereas such a region of thick-walled cells normally is discernible in *Lepidozia* (Figs. 6 : 13; 8 : 9; 9 : 14; 10 : 15).

4. Leaves in *Lepidozia* are usually much less deeply divided (usually for less than 0.55 their length) than in *Telaranea,* although some taxa of the latter (e.g., *T. centipes;* cf. Figs. 3 : 1, 7; 4 : 2) may have less deeply lobed leaves. Even in this last species, lobes are only inserted on 2 basal cells and are uniseriate distally, a tendency expressed more fully in *T. nematodes* and *T. mooreana* (cf. fig. 90 : 10–12 in Schuster, l.c., and Fig. 2 : 2, 3, this paper). By contrast, in *Lepidozia,* except in the highly derived subg. *Cladolepidozia,* leaf lobes tend to be much broader, typically triangular, and fail to end in ciliiform apices, and they are never ciliiform throughout; this is true of the generitype, *L. reptans* (cf. fig. 86 : 4 in Schuster, l.c.).

5. Leaf cells in *Lepidozia* are almost without exception perceptibly firm-walled and, in the lamina and usually into the lobes, are irregularly oriented, irregularly polygonal, and never consistently elongated (Figs. 8 : 8; 12 : 1; 13 : 9); this is true even of weaker taxa such as the type, *L. reptans* (cf. fig. 86 : 4, 6 in Schuster, l.c.). In *Telaranea,* leaf cells are usually consistently thin-walled and in the lamina and/or lobe bases tend to be oriented in longitudinal lines and are mostly perceptibly tiered, as, for example, in *T. centipes* (Figs. 3 : 2, 3, 7; 4 : 2) and *T. tuberifera* (Fig. 5 : 5, 7).

[6] In *L. microphylla,* cortical cells are both larger and thinner-walled than the much smaller, thick-walled, 1–3 strata of cells lying immediately within (Fig. 9 : 14).

The cells in *Lepidozia* are not only usually somewhat firm-walled (*L. reptans,* the generic type may have them minimally incrassate; cf. fig. 86 : 6 in Schuster, l.c.), but they average much smaller than in *Telaranea* species and seem more chlorophyllose. In *Telaranea* the relatively large and thin-walled cells seem more subhyaline in most of the taxa. As a consequence, *Lepidozia* species are usually firmer than those of *Telaranea.* The cells in the lamina of *Telaranea* are often more rectangulate (Fig. 2 : 3) and are often, if imperfect, tiered; when not clearly tiered they are often clearly 5–6-angled (Figs. 1 : 1–5; 3 : 1; 4 : 2). They are always clearly angulate. Those of *Lepidozia* are much less rectangular or angulate, are only sporadically elongated, and are never clearly tiered (Figs. 6 : 1–3, 5–6, 10; 12 : 1). In practice, the cell differences between the two genera are readily perceived.

6. The ♀ bracts in *Lepidozia,* with very isolated exceptions, have a very high lamina (Figs. 7 : 5; 15 : 2), often longer than broad, and have reduced lobes; often the bracts are merely lobulate at their apices, as in the type, *L. reptans* (fig. 87 : 6–7 in Schuster, l.c.). In *Telaranea* the bracts, like the leaves, tend to be deeply lobed and sometimes bear accessory lobes and/or cilia or lacinia, as in *T. nematodes* (cf. fig. 89 : 9 in Schuster, l.c.).[7]

7. Spores in *Lepidozia* species always appear to be papillose or bear irregularly coalescent papillae, forming short, vermiculate markings (as in *Lepidozia fugax,* p. 66; *L. hirta,* p. 87; *L. kirkii,* p. 84; *L. microphylla,* p. 30; *L. obtusiloba,* p. 45; *L. pumilla,* p. 79; and *L. setigera,* p. 39). In *Telaranea* the spores are always delicately areolate (as in *T. nematodes;* cf. fig. 90 : 4 in Schuster, l.c.). The spore differences appear to be absolute: even in taxa like *L. kirkii,* in which spores may show a marked tendency for the papillae to coalesce to form vermiculate "ridges," these ridges may fork, but never delimit areolae.

In view of the considerable intrageneric variability in criteria 1–6, the differences in spore "ornamentation" seem to be of major significance in separating the two genera. Unfortunately, they have not been observed in more than a dozen taxa.

[7] The difference is far from absolute. Thus *T. centipes* has shallowly lobed or lobulate bracts (Fig. 4 : 10, 12), much like the typical condition in *Lepidozia.* Also, in *Lepidozia setigera* ♀ bracts are deeply lobed or laciniate (Fig. 12 : 3).

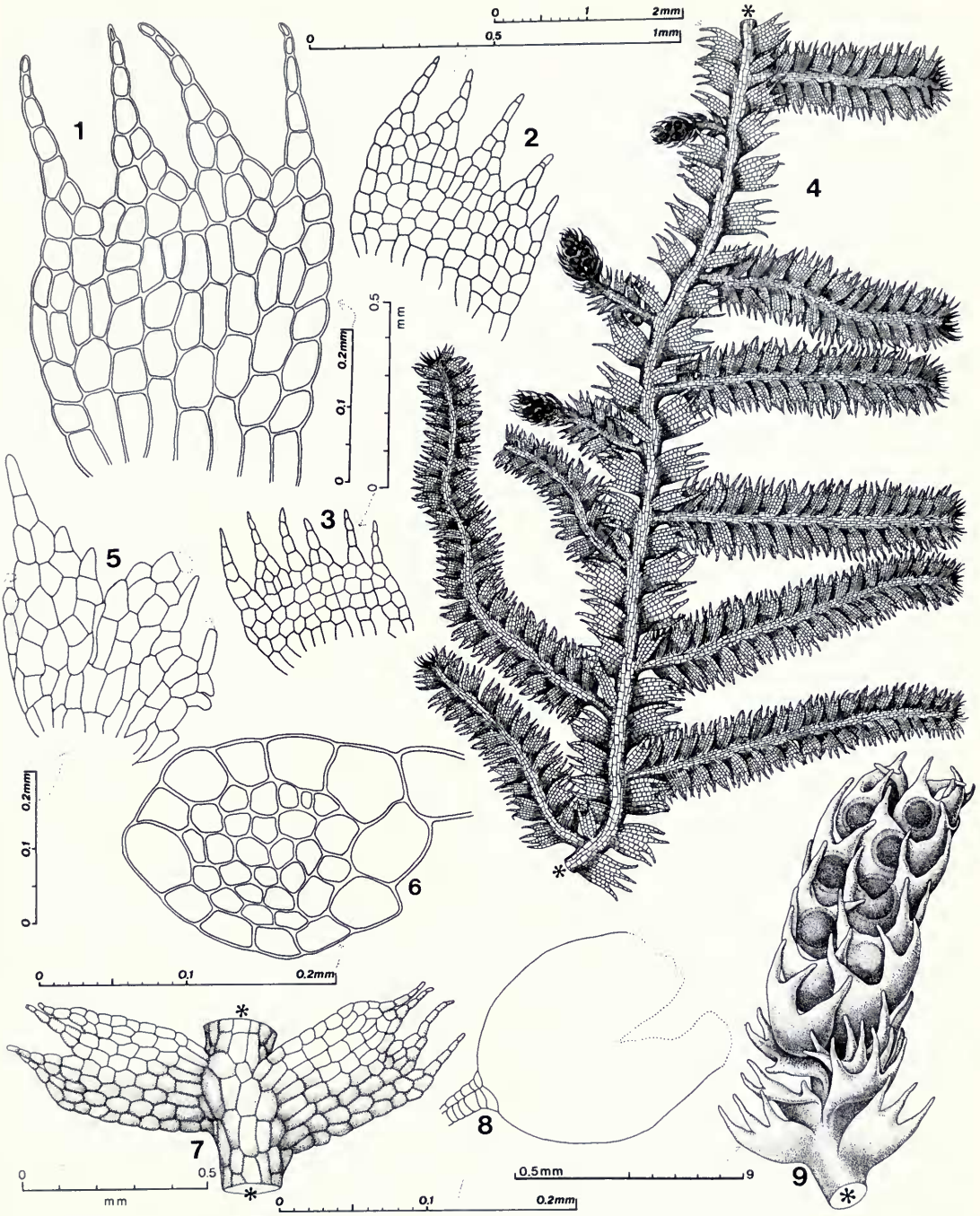

FIG. 3. *Telaranea centipes* (Tayl.) Schust. **1.** Leaf of main shoot. **2, 3.** Leaves of main shoot. **4.** Plant with 3 androecia-bearing *Frullania*-type branches. **5.** Male bract. **6.** Stem, cross section. **7.** Opposing leaf pair of main shoot, dorsal view. **8.** Antheridium. **9.** Androecial branch. **10.** Median lobe of leaf. (Figs. 1, 4–9 from *Engel 15593,* Tasmania, track from Ferndene to Mt. Dial; 2, 3, 10 from *Engel 15191,* Tasmania, Lillydale Falls.)

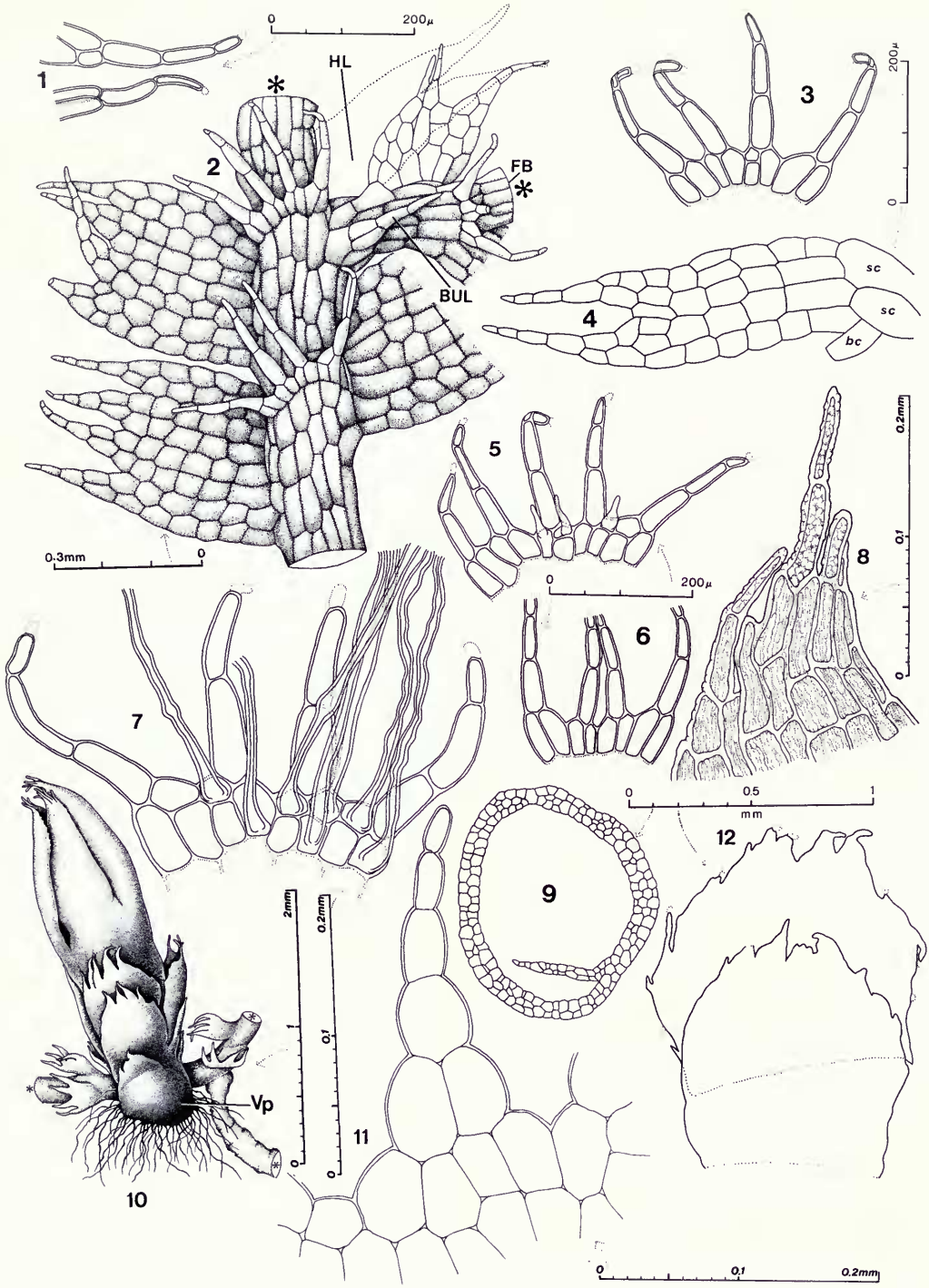

FIG. 4. *Telaranea centipes* (Tayl.) Schust. **1.** First branch underleaves. **2.** Portion of main shoot with branch, ventral view (BUL = first branch underleaf; FB = *Frullania*-type branch; HL = half-leaf, shown in outline). **3, 5–7.** Underleaves from leading shoots, stem cells stippled (note insertion of 3 young rhizoids in Fig. 5 and of mature rhizoids in Fig. 7). **4.** Half-leaf (sc = subtending stem cell; bc = subtending branch cell). **8.** Portion of perianth mouth showing cuticular detail. **9.** Perianth, cross section through median third. **10.** Perianth bearing shoot. **11.** Female bract (left) and bracteole (right) of innermost series. (Figs. 1–7 from *Engel 15593,* Tasmania, track from Ferndene to Mt. Dial; 8–11 from *Engel 15191,* Tasmania, Lillydale Falls.)

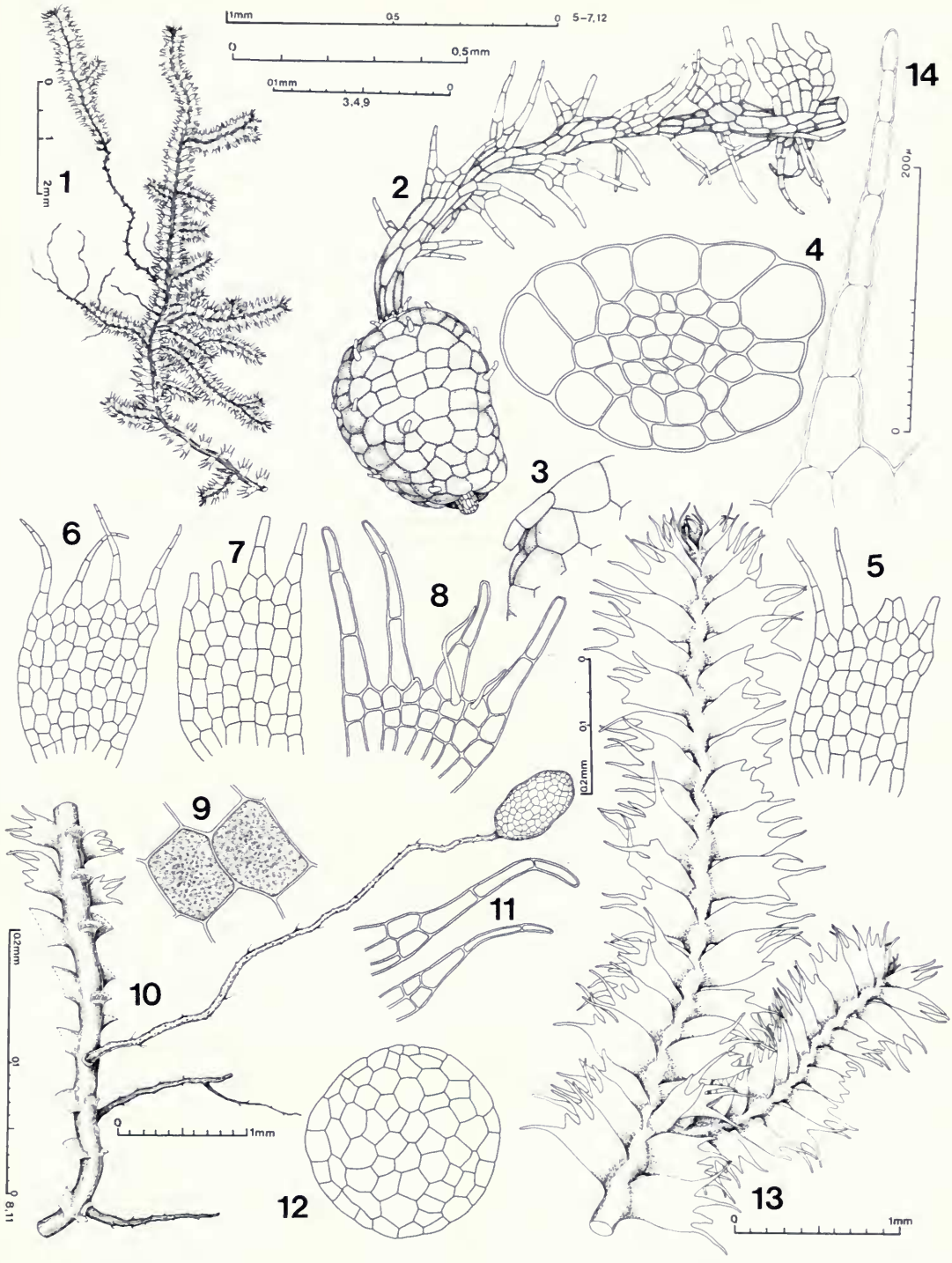

FIG. 5. *Telaranea tuberifera* Engel & Schust. **1.** Plant, dorsal view. **2.** Germinating tuber; note scattered leaf rudiments and previous point of attachment of tuber to stolon at opposing end of tuber. **3.** Portion of tuber surface showing a leaf rudiment. **4.** Stem, cross section. **5–7.** Leaves. **8.** Underleaf; note rhizoid position. **9.** Median discs cells showing cuticular detail in part. **10.** Old, basal portion of shoot showing stoloniferous branches and a tuber. **11.** First branch underleaves. **12.** Tuber, cross section. **13.** Portion of main shoot; note ragged leaf apices. **14.** Median lobe of leaf. (All from type of *T. tuberifera*.)

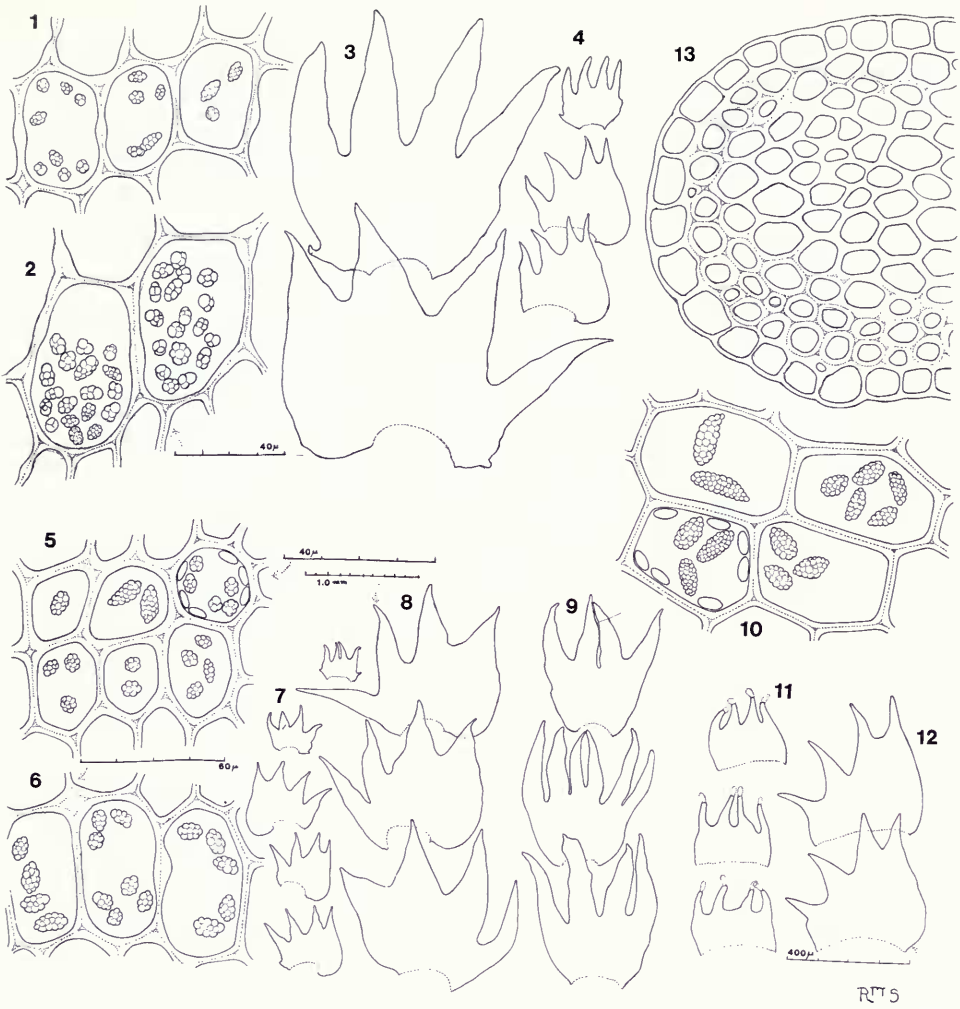

FIG. 6. *Lepidozia pendulina* (Hook.) Lindenb. (1–3 and 8–9; *Schuster 67–238*); *Lepidozia concinna* Col. (4–7; *Schuster 67–237a*); *Lepidozia microphylla* (Hook.) Lindenb. (10–13; *Schuster 67–237c,* Westland). **1.** Median cells with oil-bodies (×432). **2.** Basal leaf cells (×370; 40 μm scale). **3.** Underleaf (top) and stem leaf (×20). **4.** Two leaves and, top, underleaf; to scale of Fig. 3 (×20). **5.** Median cells with oil-bodies and (upper right) chloroplasts (×325; 40 μm scale). **6.** Basal cells with oil-bodies (×272; 60 μm scale). **7.** Two underleaves + three leaves (×15.7; 1 mm scale). **8.** Three leaves (×15.7; 1 mm scale). **9.** Three underleaves (×15.7; 1 mm scale). **10.** Median cells with oil-bodies + chloroplasts (×650). **11.** Underleaves (×40.5; 400 μm scale). **12.** Leaves (×40.5; 400 μm scale). **13.** Stem cross section.

INTRAGENERIC CLASSIFICATION—The intrageneric classification and phylogeny of the genus *Lepidozia* remain poorly understood. Study of a wide array of taxa has led Schuster (2000, pp. 183–207) to divide the genus into six subgenera, each with 1–5 sections. What follows is tentative, in part because the sporophyte generation of so few taxa is known. Nonetheless, it is clear that the genus consists of an array of relatively well-defined groups (subgenera, sections). The aspect of, for example, *Lepidozia reptans* and *L.* (*Chaetolepidozia*) *pinnaticruris* (cf. fig. 64, Schuster, 2000) and *L.* (*Cladolepidozia*) *bursifera* (cf. fig. 66A, Schuster, 2000) is so different that initially, one might consider placing them in different genera. Fulford (1966, p. 181) states that "unlike *Bazzania,*" *Lepidozia* "does not consist of obvious, well-marked groups or sections." We are impressed, on the contrary, with the relatively marked homogeneity of *Bazzania* (and cannot recognize subgenera within it) versus the perceptible heterogeneity of *Lepidozia.* Students of the ho-

larctic flora tend to conceptualize *Lepidozia* by *L. reptans;* as we show elsewhere (p. 31), this is highly atypical of the genus and should not serve as a "model" for the genus.

We assume that erect growth, branching malleability, weakly asymmetrical leaves, and transverse leaf orientation are all signs of "primitivity"; on these bases, subg. *Dendrolepidozia* is primitive. With the exception of only one other occurrence, it is the only element in the genus in which, at least sporadically, terminal branches occur from all three merophyte rows. In Schuster (1980), it is proposed that the most generalized element within the allied genus *Kurzia* is formed by *K. mollis* (Steph.) Engel and Schust. and *K. setiformis* (De Not.) Engel & Schust., taxa in which branching is "highly plastic"; in the first of these taxa also we have seen occasional ventral-terminal (*Acromastigum*-type) branches. In these species also, leaves are very deeply quadrifid, with a low disc and tapered, narrow lobes, exactly as in *Lepidozia* (*Dendrolepidozia*) *spinosissima.* In both of these taxa the leaves are slightly asymmetrical, with longer dorsal margins (and lobes) (compare Figs. 7 : 9 and 8 : 3, 4, 10 in this paper with fig. 1 : 8 in Schuster, 1980). Both taxa have leaves that are almost transversely inserted; leaves and underleaves tend to be similar; the latter tend to be more than two-thirds the area of the former. The erect growth of *Dendrolepidozia* also may be considered a primitive feature. Interestingly, *Acromastigum*-type branching occurs again only in *L. pumila* (Fig. 29 : 3), a species of the relatively derived sect. *Notholepidozia.* The presence of ventral-terminal branching in *L. pumila* is all the more remarkable because it occurs in a plant with a closely prostrate habit.

Taxonomic Sequence Adopted—We start our treatment with *Dendrolepidozia* because of the features emphasized above. In the erect, almost "woody" axes, *Dendrolepidozia* seems allied with *Mastigolepidozia* (the *L. microphylla* element), and we treat this group next.[8] Both of these groups show copious branching, and they are regularly 2–3-pinnate. By contrast subg *Notholepidozia* consists basically of loosely prostrate plants (becoming suberect only when crowded), with a stem usually showing slight cortication. In this subgenus anisophylly is usually marked; the leaves are usually strongly incubous, often with deflexed apices. Branching in subg. *Notholepidozia* is generally once-pinnate, with branches typically of limited length (unless they end in flagella; in this case, they often bear secondary branches). This is clearly seen in the generic type, *L. reptans* (cf. fig. 86 : 7, 9, in Schuster, 1969).

Subgenus *Notholepidozia* also shows a series of derived tendencies: Some taxa develop strong dentition of the leaves; others develop strikingly ampliate dorsal leaf bases; some develop cuticular ornamentation. Subgenus *Notholepidozia* is therefore treated as third in a linear arrangement, although we do not wish to imply that *Mastigolepidozia* "gave rise" to subg. *Notholepidozia.*

Subgenus *Glaucolepidozia* is treated last in our arrangement, for several reasons. It is highly derived in the peculiar cutinization, which gives the plants a striking opaque, whitish aspect not seen in any other taxa of *Lepidozia.* In other respects, it is relatively close to subg. *Lepidozia,* for example, in its creeping growth, its leaf and underleaf form, and its ramification. Subgenus *Glaucolepidozia* is derived in its leaf cells. These are mostly equally firm-walled, very chlorophyllose, and have few, very small, mostly few-segmented oil-bodies, always smaller than the chloroplasts (Figs. 36 : 9, 10; 38 : 8–10).

Subgenus *Austrolepidozia,* with only *L. ulothrix,* also represents a highly derivative element. It has ciliate to spinose-ciliate leaf margins, much as in *Chaetolepidozia;* as in that subgenus, cilia are formed of strongly elongated, thick-walled cells. In *Austrolepidozia,* cilia are usually alternate, more sporadically opposed; in *Chaetolepidozia,* each lobe typically bears two to three pairs of opposed cilia. *Austrolepidozia* approaches subg. *Lepidozia* in the strongly asymmetrical leaves that are relatively shallowly lobed (Figs. 33 : 3–5; 34 : 1, 2).

The two subgenera not regionally represented, *Cladolepidozia* and *Chaetolepidozia,* would naturally fall last in any linear arrangement; both are highly derived groups. In *Cladolepidozia,* leaf lobing is greatly reduced, and the vestigial lobes are represented by mere cilia (as in *L. cladorhiza* (Reinw. et al.) G. L. & N; see Schuster, 2000, figs. 65 and 66, and Piippo, 1984, fig. 6 : a–g) or coarse, serrate teeth (as in *L. ferdinandi-muelleri* Steph.; see Piippo, 1984, fig. 6 : h–n; Mizutani, 1968, fig. VI). Some taxa in this subgenus have ampliate leaf- and underleaf-bases, converted into water sacs (see Grolle, 1967, fig. 2, and Schuster,

[8] There is also a clear similarity (and presumable affinity) in the "woody" main stem, the transversely oriented leaves, and the virtual isophylly to the otherwise highly derivative subg. *Cladolepidozia* (compare figs. 65, 66, and 66A in Schuster, 2000).

2000, fig. 66A of *L. bursifera* Hatt. & Grolle). In *Chaetolepidozia* the deeply lobed leaves and underleaves are armed with several pairs of spinescent teeth and/or cilia (see Schuster, 2000, fig. 64), much as is typical of, for example, *Temnoma* and *Trichocolea* (as in *L. lacerifolia* Steph.; see Piippo, 1984, fig. 8 : a–b). This last subgenus is known only from gametophytic plants, and indeed, discovery of sporophytic material may necessitate removal of the subgenus from *Lepidozia* and its elevation to generic status. Both *Cladolepidozia* and *Chaetolepidozia* have almost "woody" main stems, 20–24 cells high, with 3–5 strata of thick-walled cells peripherally, forming a rigid cortex (figs. 64 : 9; 66A : 13, Schuster, 2000). Such rigid stems are approached, in our taxa, only by *L. pendulina* (Fig. 10 : 15) and *L. microphylla* (Fig. 9 :14).

After much deliberation, we have excluded subg. *Lepidozia* in our treatment. That subgenus is exclusively Laurasian; it has consistently tiny, homogeneous, smooth (rarely with an "appendix" cut-off) and numerous oil-bodies per cell (p. 16). In all Australasian taxa we have studied, oil-bodies are fewer per cell, relatively large, and consistently coarsely botryoidal (Fig. 6 : 1, 2, 5, 6, 10); cf. p. 16.

The bulk of taxa thus belong in subg. *Notholepidozia.* This remains relatively heterogeneous and, after a suite of sporophytes has been adequately studied, may possibly be subject to subdivision.

The perimeters of the subgenus emerge from the conspectus (p. 18) of subgenera, modified from Schuster (1973, 2000).

Taxonomic Characters and Morphology

Branching, Form, and Orientation of Basal Branch Underleaves—In general, the first underleaf formed on a *Frullania*-type branch differs substantially from succeeding branch underleaves. Usually the initial branch underleaf is so oriented that it is not "in line" with succeeding branch underleaves; it is often displaced so that it is more nearly in line with lateral stem leaves. In most taxa the initial branch underleaf is substantially smaller (and often has fewer lobes) than stem and branch underleaves distad of the basal one.

In *L. kirkii* (Fig. 31 : 3, 4), however, the basal branch underleaf is nearly identical to succeeding branch underleaves, aside from usually being 3- rather than 4-lobed; it is oriented in line with succeeding branch underleaves.

In *L. spinosissima* the basal branch underleaf is normally 2–3 lobed and narrower than successive 4-partite underleaves (Fig. 7 : 11); it is oriented so that it is not quite in line with successive underleaves (Fig. 8 : 1, 2), and the branch superficially appears almost axillary to it. Such displacement of the initial branch underleaf is typical of most taxa. Thus in *L. acantha* and *L. elobata* the first branch underleaf is displaced and is 1-segmented, versus the 4-segmented succeeding branch underleaves (Fig. 27 : 3, 5).

In related taxa, the first branch underleaf may be a useful character. The consistently monocrurous condition in *L. acantha* and *L. elobata* is unique in sect. *Notholepidozia.* Moreover, the shape of the first branch underleaf is different between these species: subulate in *L. acantha* (Fig. 27 : 3, 5), versus ovate-lanceolate in *L. elobata* (Fig. 28 : 1, 2). However, the first branch underleaf of related taxa, clearly of the same species complex, may be variable and therefore of little taxonomic utility. Thus, in *L. novae-zelandiae* the initial branch underleaves range from (1)2 to 3(4)-lobed, and may be 1–2-fid even on a single stem (Fig. 26 : 7). In the allied *L. pumila,* initial branch underleaves are (1)2–4-fid and may be 2–4-lobed even within the same population (Fig. 29 : 2, 3, 11, the type).[9]

Stem Anatomy—The generic type, *L. reptans,* has ca. 20–24 rows of cortical cells that are slightly to moderately larger than the medullary cells; the medullary have walls scarcely more firm-walled than the cortical (fig. 87 : 8 in Schuster, 1969). A cortex is hardly differentiated.

In New Zealand taxa there is wide variation in (a) degree of differentiation of a hyaloderm and (b) degree of rigidity of the medulla, depending on how strongly thick-walled the outer and sometimes the inner strata of medullary cells are. The following general types exist:

1. In the most vigorous taxa, such as *L. pendulina* (Fig. 10 : 15), a hyloderm hardly exists; some 5–8 outer strata are thick-walled, and the outermost layer is not differentiated as a hyaloderm. The central medulla consists of thin-walled cells.

[9] A cautionary note: Initial branch underleaves and their number of lobes may reflect vigor of the shoot. Thus, in *L. concinna* the lower, weaker shoot sectors may have 3-fid basal branch underleaves; the vigorous distal shoot sectors have them (3)4-fid (Fig. 19 : 1, 1A).

2. In *L. microphylla* the main axis is rigid, as in *L. pendulina,* and is ca. 22–26 cells in diameter (Fig. 9 : 14). Here the peripheral stratum is differentiated as a recognizable hyaloderm, and 2–4 strata within are of smaller cells, with rather firm walls.

3. In *L. spinosissima* (Fig. 8 : 7, 9) the main axis is much as in *L. microphylla:* a weakly differentiated hyaloderm, with several strata of smaller thick-walled cells within that grade into a larger-celled medulla.

These taxa and *L. kirkii* (Fig. 31 : 10) agree in having rather massive stems, with numerous rows of cortical cells.

4. Within the more reduced taxa, such as *L. acantha* (Fig. 27 : 2) and *L. novae-zelandiae* (Fig. 26 : 13), we see progressive reduction in axial complexity. An ultimate point is reached in *L. novae-zelandiae* var. *minima,* with the stem only ca. 6–7 cells in diameter (Fig. 26 : 13). Stems of var. *minima* have slightly larger cortical cells that are strongly thick-walled, much as the cells within, which average rather smaller in diameter.

In general, there is a correlation between vigor, erect growth, and evolution of a relatively "woody" stem, as in *L. microphylla.* Smaller taxa, especially if not developing a stiffly erect main axis, tend to have weaker stems, with less histological differentiation. Thus in *L. acantha* (Fig. 27 : 2) and the allied *L. laevifolia* (Fig. 22 : 12), stems with a fundamentally similar anatomy are found. The cortical and medullary cells in *L. laevifolia* are considerably firmer-walled than in *L. acantha.*

In virtually all the cases cited there is a weakly to at most moderately differentiated hyaloderm of larger, usually more leptodermous cells, contrasted to a medulla in which at least peripheral strata are firm to thick-walled. In subg. *Glaucolepidozia,* however, the stem is formed of thin-walled or virtually thin-walled cells throughout, and the cortical cells are hardly differentiated (at least in cross section) from the medullary cells (Figs. 36 : 11; 37 : 7; 38 : 7).

We have illustrated the axial anatomy of a range of species but have de-emphasized axial anatomy in the taxonomic treatment because, aside from the four general types (1–4, above), the degree of histological differentiation in the stem reflects, in part, overall gametophyte size. Thus, vigorous main axes in *L. microphylla* (Fig. 9 : 14) have stems ca. 22–26 cells in diameter, versus only ca. 12 cells high on axes of weaker plants (Fig. 6 : 13).

Ventral Merophyte Width—In the generic type, *L. reptans,* ventral merophytes are ca. 5 cell rows broad (Schuster, 1969).

Austral taxa exhibit a broad range of merophyte width, a character best observed in material cleared in Hoyer's fluid. Some taxa have many cell rows (e.g., *L. microphylla, L. pendulina*), and merophyte width data are not cited under such species. In the smaller taxa, however, merophyte width is typically fixed and may be useful in species discrimination.

Thus, in the complex centering on *L. novae-zelandiae, L. acantha,* et al. (sect. *Notholepidozia*), ventral merophytes may be only 4–5 cell rows broad (*L. novae-zelandiae;* Figs. 24 : 14; 26 : 13), ranging to 5–6 rows (*L. pumila,* Fig. 29 : 10), to 7 in *L. fugax* (Fig. 23 : 10), to as many as 8 rows in *L. laevifolia* (Fig. 20 : 11). Ventral merophyte width is used to differentiate between species pairs within the key. For example, *L. bidens* has ventral merophytes 8 cells across (Fig. 30 : 10) versus 5–6 cells in *L. pumila;* the character also is used in the couplet distinguishing *L. fugax* from *L. novae-zelandiae. Lepidozia concinna,* also of sect. *Notholepidozia,* has ventral merophytes 10 cells broad (Fig. 18 : 11).

All species within subg. *Glaucolepidozia* differ at least in the range of ventral merophyte width. The widths range from 3–4 cells across (*L. digitata*), to 4–6 (*L. glaucescens*), to 8–9 (*L. glaucophylla*), to 9–10 (*L. bisbifida*). In the key, the widths easily separate *L. bisbifida* from *L. digitata.*

Leaves—Leaves of *Lepidozia* may be subsymmetrical or weakly asymmetrical, as in *L. spinosissima* (Fig. 7 : 9) or *L. acantha* (Fig. 27 : 6), but typically they are moderately to strongly asymmetrical. Such leaves have the dorsal margin of the disc longer than the ventral margin. The longer margin is often accompanied by various degrees of dilation of the dorsal sector of the leaf; examples are *L. setigera* (Fig. 11 : 3, 4) and *L. procera* (Fig. 13 : 5, 7).

Leaves in *Lepidozia* typically are 4-lobed, although in some taxa sporadic 3- and 5-lobed leaves occur. The sinuses usually descend for less than 0.55 their length, although exceptions are present, for example, in *L. spinosissima,* where leaves are divided to 0.7–0.9 (Fig. 7 : 9). The distance from the dorsal sinus base to the leaf insertion is at times much greater than from the ventral sinus to the insertion. This occasionally results in the dorsalmost two lobes being conspicuously paired (e.g., *L. bidens,* Fig. 30 : 2, 3). The differ-

ences in distance between sinus base and leaf base often correlate with the degree of leaf asymmetry. Thus, the conspicuously shallow dorsal sinus of *L. procera* accompanies a strongly asymmetrical leaf (Fig. 13 : 5, 7). The dorsal sinus in *L. obtusiloba* is exceptionally shallow, and in this species it may be reduced to a mere notch (Fig. 14 : 1).

Leaves of New Zealand *Lepidozia* species are typically devoid of teeth, although some species may at times have the dorsal margin of the disc armed with a few distant, irregular, few-celled teeth (e.g., Fig. 35 : 7, 9, of *L. glaucophylla*). However, conspicuous leaf margin ornamentation occurs in two groups. Subgenus *Austrolepidozia,* with *L. ulothrix,* has leaf lobes with up to 10–12 cilia, usually oriented in opposed pairs (Fig. 34 : 2, 6). Also, the dorsal margin and the confluent margin of the dorsal lobe have up to 12–19 spinose teeth or cilia. Members of sect. *Kirkii* have the dorsal margin of the disc and the dorsal 1–2 lobes coarsely and variably toothed (Figs. 31 : 1; 32 : 2, 4, 10).

Leaf Cells, Cuticle, and Oil-Bodies—Leaf cells in *Lepidozia* are typically firm-walled; and, at times, well-developed trigones may be present (as, for example, in *L. concinna* (Fig. 18 : 6) and *L. ornata* (Fig. 17 : 12). However, some of our New Zealand species may have uniformly thin-walled cells, and it is not altogether surprising that species with such cells are found in sheltered, deeply shaded loci such as cavelike recesses at cliff bases or in pockets at tree bases. *Lepidozia digitata* is an example (Fig. 38 : 9, 10). *Lepidozia reptans,* the generitype, has cells minimally incrassate (cf. fig. 86 : 6 in Schuster, 1969). Leaf cells in *Lepidozia* are irregularly arranged, irregularly polygonal in shape, and never consistently elongated.

The ornamentation of the cuticle is a significant character within *Lepidozia.* Plants of subgenus *Glaucolepidozia* have a dull, water-repellent surface due to the presence of a waxy cuticle. The leaves and stems of such plants are opaque, whitish, and glaucous, sometimes becoming pale brownish with age. Some *Lepidozia* species have papillose lobes but a smooth disc (Fig. 23 : 4, *L. fugax*), while others have both lobes and disc papillose (Fig. 27 : 7, 8, *L. acantha*). The character is particularly useful in distinguishing the smaller species of sect. *Notholepidozia.* For example, distinctly papillose leaves occur in *L. laevifolia* (Fig. 20 : 8–10) and *L. novae-zelandiae* (Fig. 24 : 6), whereas leaves are smooth (or at most faintly and indistinctly papillose) in *L. pumila* and *L. bidens.* Care is required in the use of this character, because ornamentation at times is subtle and rather difficult to observe. For this reason, it is recommended that several leaves, particularly from several different shoots, be routinely checked for presence versus absence of cuticle features.

We have studied the oil-bodies of some 5–6 taxa of subg. *Notholepidozia.* They are consistently relatively few per median cell (usually 2–7(8) in *L. pendulina* and 1–5 per cell in *L. concinna*) and are always distinctly, if not coarsely, botryoidal. In subg. *Mastigolepidozia* (*L. microphylla*) they are somewhat less coarsely botryoidal, average rather larger than in *Notholepidozia* species studied, and occur 2–5 per median cell (Fig. 6 : 10). Only in subg. *Glaucolepidozia* do we see very different, often vestigial oil-bodies (cf. p. 92 and Figs. 36 : 9; 38 : 10).

By contrast, all workers find that the generic type, *L. reptans,* has homogeneous oil-bodies (Hattori, 1953; Schuster, 1969, fig. 86 : 6; Furuki & Higuchi, 1997). Similar oil-bodies are reported for the other two Asiatic taxa, *L. robusta* and *L. subtransversa* (Furuki & Higuchi, l.c.). In these three taxa, oil-bodies are more numerous: 5–16 per cell in *L. reptans* (Schuster, 1969; Furuki & Higuchi, l.c.) and 5–15 or 5–20 per cell in *L. robusta* and *L. subtransversa* (Furuki & Higuchi, l.c.). In none of the holarctic taxa studied did we ever see 2–4 or 2–5 oil-bodies per cell, typical of the New Zealand species studied (cf. Fig. 6 : 1, 5, 10). Only in basal cells (as of *L. pendulina;* Fig. 6 : 2) may there be more numerous oil-bodies, but in other taxa (e.g., *L. concinna*), there may be only 4–8 per basal cell (Fig. 6 : 6). The taxonomic implications of these observations need to be buttressed by in-depth studies of a wider range of taxa. They strongly suggest that the internal classification of *Lepidozia s. lat.* needs intensive study.

Asexual Reproduction—Asexual reproduction is sporadically present in our *Lepidozia* species and occurs by fragmenting or caducous leaf lobes, whose bases persist as truncate stubs. Caducuous leaf tips are found in *L. fugax* (Fig. 23 :1, 3, 5) and give the plants a distinctive ragged appearance (for details, see Differentiation section under that species, p. 66). *Lepidozia fugax* is the only regional representative of subg. *Notholepidozia* with asexual reproduction. At least the weaker phases of *L. digitata* (subg. *Glaucolepidozia*) may have fragmenting or irregularly caducous leaf lobes (Fig. 38 : 1, 3, arrows), and

even underleaf lobes may be caducous. Dissemination presumably is by such leaf fragments.

ANDROECIA—Although the generitype (*L. reptans*) is autoecious, the vast majority of species within the genus are dioecious. Androecia occur on short, spicate, often cernuous, determinate, ventral-intercalary branches devoid of normal leaves and underleaves (Fig. 7 : 2) and are typically found in the median or basal sectors of a shoot. (Figure 7 : 1 shows androecia on the primary and secondary branches of the median sector of the plant.) In some species, androecia also occur terminal on primary and secondary branches. Regardless of position, the androecia are inconspicuous, and those of the main shoot may not exceed the tips of the underleaf lobes, as in *L. ulothrix*.

The androecia are rather uniform and do not yield characters of taxonomic significance at any level. Bracts are bifid to at most 0.4, with acute to acuminate lobes. The dorsal margin is entire or may have a tooth, and several slime papillae may be present, with or without the tooth. The dorsal margin in several unrelated species (*L. ornata, L. ulothrix, L. bisbifida*) is dilated, forming a moderately rounded projection (Fig. 34 : 12, *L. ulothrix*).

GYNOECIA—The abbreviated gynoecial branches in *Lepidozia* have several progressively larger gyres of bracts and bracteoles (Fig. 16 : 1, *L. obtusiloba*). The lowermost gyre typically consists of inconspicuous scalelike bracts and bracteoles, while the inner 1–2 gyres are erect, concave, and sheath the lower part of the perianth (Fig. 7 : 4, *L. spinosissima*). In general, in *Lepidozia* the ♀ bracts are strongly differentiated from leaves in both form and size and are subisophyllous to isophyllous (Fig. 7 : 5, *L. spinosissima;* Fig. 15 : 2, *L. obtusiloba*). The generic type, *L. reptans,* has very large bracts and bracteoles, with the apices usually 4-lobulate (Schuster, 1969, fig. 87 : 6, 7). The ♀ bracts and bracteoles in most of our taxa are shallowly 4- (exceptionally 5- or 6-) lobate to lobulate, as in, for example, *L. spinosissima* (Fig. 7 : 4, 5). They are particularly shallowly lobed in *L. obtusiloba* (Fig. 15 : 2, 3), and in this species the bracts may occasionally have obsolete lobes, with each represented solely by a slime papilla mounted on 2 laterally juxtaposed cells that project slightly more than the neighboring cells (Fig. 15 : 2, bract at left, 4). In *Lepidozia laevifolia* the bract summit may have 4 small teeth that are hardly differentiated from the otherwise crenate-denticulate apex (Fig. 21 : 2).

There are, however, two notable deviations from this general pattern. First, in *L. setigera* the bracts and bracteoles are 4-partite for ca. 0.4–0.5 their length and are much less elongated than in the preceding taxa cited (Fig. 12 : 3). Second, gynoecial bracts may have only 2 teeth or lobules, as in *L. pumila, L. bidens,* and *L. hirta,* but in all of these species, 4 dentate-lobulate bracts are also present. Bracts with 2 short lobes at times are present in *L. laevifolia* (Fig. 21 : 3).

Characters involving bract lobe and lamina margins are not of taxonomic significance, although differences exist between some species. The lobes typically are composed of ± regularly rectangular and (particularly toward the lobe margins) irregularly sinuate-rhomboidal cells. The apical end of the lobe marginal cells is frequently thickened and variously diverging, often only feebly so, as in *L. obtusiloba* (Fig. 15 : 3). In other instances the cells markedly diverge and result in a crenate to denticulate lobe margin (Fig. 7 : 6, *L. spinosissima*).

Bract lamina margins are bordered by cells variable in shape and orientation, often thinner-walled, typically narrowly elongated, and often ± sinuate-rhomboidal in shape. The apical or free end of the marginal cells in most species is variously divergent and forms a short projection or a tooth, and in such cases an irregularly crenulate to crenate-denticulate margin results. In some species, ornamention is primarily in the distal half of the lamina margin (Fig. 7 : 5, *L. spinosissima*); in others, the margins are ornamented to the base (*L. laevifolia,* Fig. 21 : 5). The apical end of the marginal cells is exceptionally nonprotuberant, a condition that results in an esentially smooth margin, as in *L. obtusiloba* (Fig. 16 : 5), although the margins of this species may occasionally be crenulate-denticulate by variously projecting cells (Fig. 16 : 1).

Perianths are fusiform or ellipsoidal-fusiform in shape (Figs. 7 : 4; 15 : 1) and are terete in the median and basal sectors (Figs. 7 : 7a; 15 : 9); the cylindrical sector of the perianth is (2)3-stratose (Fig. 15 : 8b, m). Perianths become narrowed and bluntly 3-gonous distally (Fig. 7 : 7b, c) and deeply plicate for varying distances just below the mouth. The perianth also becomes unistratose distally (Fig. 15 : 8d, d′). The perianth mouth in most of our species is shallowly 3-lobed, with the lobe margins composed of irregularly sinuate-rhomboidal cells (Fig. 15 : 6). These mouth cells are laterally free for varying lengths at the apical end, and only rarely are completely free laterally. This

condition results in the prevailing crenate-denticulate mouth. Examples of exceptions to this condition follow. The perianth mouth in *L. spinosissima* is shallowly lobulate (not divided into 3 lobes), and the teeth of the mouth are composed of a single cell or a uniseriate row of at most 3 cells (Fig. 7 : 8), with the teeth thus being more protracted than in most species. The perianth of *L. laevifolia* is shallowly 3-lobed, and the mouth crenate-denticulate, with mouth cells laterally free for varying lengths at the apical end (Fig. 21 : 6, 7). The shallowly 3-lobed perianth of *L. obtusiloba* has mouth cells laterally fused to the summit or nearly so, and the mouth is thus merely regularly crenulate (Fig. 15 : 6, 7).

The calyptra extends ca. 0.5 the perianth length, and no evidence is present of stem calyptra development (the unfertilized archegonia remain at the extreme base of the calyptra).

Seta Anatomy—In Schuster (1969, p. 17), the seta of *Lepidozia* is stated to be "where known of *12 or more rows of epidermal cells*" (author's emphasis). The generic type, *L. reptans,* has 12 epidermal cell rows.

However, the seta has 8 epidermal cell rows in *L. laevifolia* (Fig. 20 : 12), *L. fugax,* and *L. pumila,* and 9 epidermal cell rows in *L. hirta* (Fig. 32 : 9). Several relatively vigorous species have a greater number of epidermal cell rows. Thus, *L. setigera* has 11–13 rows (Fig. 12 : 11), and *L. obtusiloba* (Fig. 16 : 2) and *L. pendulina* each have 16 rows. There seems to be at least a weak correlation between gametophytic vigor and seta anatomy. The character is used in the key to help separate *L. obtusiloba,* with 16 rows, from the taxa with 8 rows mentioned above. Seta differences also distinguish *L. kirkii* (10–14 rows) from *L. hirta* (9 rows).

Capsules—The capsule in *Lepidozia* is ellipsoidal to oblong in profile (Fig. 15 : 10, *L. obtusiloba*), and, like the seta, there seems to be a weak correlation between gametophytic vigor and the thickness of the capsule wall. Thus, smaller species, such as *L. fugax* and *L. pumila,* have 3-stratose capsule walls, whereas larger species, such as *L. microphylla* and *L. obtusiloba* (Fig. 16 : 3), have 4–5-stratose capsules, and the vigorous *L. setigera* has a 5–6-layered capsule wall. The correlation is not absolute, since *L. laevifolia,* a small species, has both 3–4- and 4–5-stratose valves (Fig. 21 : 8, 9), and *L. kirkii,* a relatively small species, has 5-stratose capsule walls. The character is used in the key to species to aid in the separation of *L. obtusiloba,* with thicker capsules, from *L. fugax* and *L. pumila.* In all *Lepidozia* species we have studied, the epidermal cells have a "two-phase" ontogeny, as defined in Schuster (1966). This is true of the generic type (fig. 87 : 3, 4, Schuster, 1969) and of studied New Zealand taxa, for example, *L. obtusiloba* (Fig. 16 : 4) and *L. laevifolia* (Fig. 21 : 10). Aside from differences in degree to which the "nodular" thickenings are developed and whether they tend to coalesce (Fig. 16 : 4) or are hardly so (Fig. 21 : 10), the genus seems singularly uniform with regard to capsule wall microanatomy.

Spores—The spores in *Lepidozia* species bear coarse, sharply defined papillae and short, vermiculate markings (Fig. 16 : 6, *L. obtusiloba*). The markings or ridges may fork, as in *L. pumila, L. kirkii,* and *L. hirta,* but do not delimit areolae.

Conspectus of Subgenera of *Lepidozia*

1. Leaves clearly, usually conspicuously (3)4(5)-lobed, devoid of water sacs; underleaves various, never with water sacs; leaves subtransverse to clearly incubous, normally conspicuously asymmetrical, not strongly narrowed to the lobe apex 2
   2. Leaves and underleaves with lobes entire-margined or variously toothed, the teeth, if present, usually broad-based, never in opposing pairs 3
      3. Leaves clearly incubously inserted, obliquely or virtually horizontally oriented, ± clearly asymmetrical, quadrilobed for under 0.6 their length; *Acromastigum*-type branches uniformly lacking (exc. in 1 species of sect. *Notholepidozia*) 4
         4. Plants devoid of a waxy cuticular covering, not wholly opaque, green to yellow-green or (rarely) brownish in life; cells quite distinct and firm in moist preparations; oil-bodies conspicuous, homogeneous or ± botryoidal, persistent, (2)4–10 or more per cell 5
            5. Plants with leaves ± imbricate, much broader than stem (very incubously inserted and oriented); branching primarily 1-pinnate (the pinnae simple or rarely with more than one secondary branch); stem with cortication weakly developed 6

6. Oil-bodies essentially homogeneous, smooth (sporadically some few septate), usually (8)10–16(23) per median cell ..... [Subg. *Lepidozia*]
6. Oil-bodies finely to coarsely botryoidal, usually 2–8 per median cell (in basal cells to 4–18 per cell) ..... Subg. *Notholepidozia* Schust.

5. Plants with leaves scalelike (especially on branches), very remote, their width not exceeding that of the stem; branching regularly 2–3-pinnate; stem strongly corticated, stiffly erect but branches drooping. (Oil-bodies usually 2–5 per cell, rather finely botryoidal.) ..... Subg. *Mastigolepidozia* Schust.

4. Plants with a waxy cuticle, whitish, opaque, glaucous, the cells obscured because of the cutinized surface; cells thin-walled; oil-bodies tiny, few-segmented, often ephemeral and obscure, usually (1)2–4(5) per cell. Plants flatly creeping, with subcontiguous to contiguous leaves ..... Subg. *Glaucolepidozia* Schust.

3. Leaves subtransversely inserted and oriented, subsymmetrical, 0.7–0.9 quadrifid (the lobes narrowly lanceolate, longly tapered); *Acromastigum*-type branches sporadic. Plants erect, dendritic, stiff, with cernuous branches, nitid ..... Subg. *Dendrolepidozia* Schust.

2. Leaves and underleaves with lobes armed with (2)3–4 or more pairs of sporadically to mostly opposed spinose or ciliiform teeth (the lower tooth sometimes elaborated as a secondary lobe). Leaves large, clearly incubuous, concave, imbricate; cuticle striolate 7

7. Dorsal sinus of leaf descending less than 0.45 the leaf length, the disc high; leaf asymmetrically ovate, length equal to or greater then lamina width; leaf lobes with 1–3(4-5) cilia, which are mostly sporadically opposed; basal branch underleaf (BUL[1]) 3–5(8) ciliate and/or lobed; stem half-leaf, associated with branch, less than 0.5 bilobed, lobes usually with cilia and/or teeth alternate ..... Subg. *Austrolepidozia* Schust.
7. Dorsal sinus of leaf descending 0.55–0.65 leaf length, the disc low; leaf (flattened) asymmetrically obtrapezoidal, length inferior to disc width; leaf lobes with 7–16 cilia, mostly in opposed pairs; basal branch underleaf deeply 2–3 fid, with copious paired cilia; stem half-leaf to 0.65–0.8 trifid, with copious cilia, mostly in pairs ..... Subg. *Chaetolepidozia* Schust.

1. Leaves not lobed at apex, the leaves merely ciliolate or ciliate at the narrowed apex, with or without an elaborated water sac at the base; underleaves ovate, broadest at base, with or without basal water sacs; leaves transverse or feebly incubous only, erect and sheathing, ovate-reniform to very broadly ovate, subsymmetrical, strongly and ± abruptly narrowed to the triangular apex, which bears merely 4 minute, uniseriate cilia (= the lobes). Cells finely papillose. New Guinea to Indomalaya ..... Subg. *Cladolepidozia* Schust.

Conspectus of New Zealand *Lepidozia* Taxa

Artificial Key to New Zealand Species of *Lepidozia*

1. Branching irregularly to regularly once-pinnate, secondary branches rarely or sporadically developed, if present only 1(2) per primary branch (branches sometimes developing into new leafy shoots); leaves imbricate to contiguous, the insertion weakly to distinctly incubous 2
   2. Plants opaque and ivory-white, becoming pale brownish with age; leaves and stems with a dull, waxy, water-repellent surface (at least on new growth) 3
      3. Dorsal margin of leaf moderately to distinctly ampliate; cells of disc and lobes not papillose (but with a fine, granular coating); leaves broadly inserted and clasping the stem, distinctly concave, with involute lobes and margins; leaf insertion strongly incubous to horizontal 4
         4. Disc cells with evenly thickened walls, trigones never present; dorsal margin of leaf strongly ampliate, distinctly auriculate at the insertion, the dorsal margin sinuate to distantly toothed; leaf lobes subcaudate, ending in a uniseriate row of 3–5 cells. Rare (South Is., Paparoa Mts.) ..... *L. glaucophylla* (p. 92)
         4. Disc cells lax, nearly thin-walled, trigones lacking to medium; dorsal margin of leaf moderately ampliate, ± clearly cordate at the insertion, the dorsal margin normally entire; leaf lobes acute to apiculate, ending in a single cell or a uniseriate row of 2–3(4) cells 5
            5. Plants medium, to 1.5 cm wide (including branches); leaves 0.8–1.3 mm long and broad, the disc 15–22 cells high at dorsal sinus, the median lobes 6–10 cells wide at base; underleaves inserted on 9–10 rows of stem cells, the disc 5–9 cells high; first branch underleaf 2- to 4-lobed, transversely inserted on the stem, often somewhat below the branch. Typically higher-elevation forests to subalpine to alpine ..... *L. bisbifida* (p. 95)
            5. Plants small, to 0.6 cm wide (including branches); leaves at most 0.55 mm long and broad, the disc 7–13 cells high at dorsal sinus, the median lobes 3–5 cells wide at base; underleaves inserted on 3–4 rows of stem cells, the disc 2–4 cells high; first branch underleaf 2-lobed (or rarely undivided), obliquely inserted at branch base. Forest plant; 950–1390 m ..... *L. digitata* (p. 98)
      3. Dorsal margin of leaf ± straight; cells of disc and lobes striate–papillose, the papillae obscured by the continuous waxy coating; leaves narrowly inserted, the disc flat, with spreading lobes; leaf insertion weakly to distinctly incubous. Disc and lobe cells distinctly thick-walled; first branch underleaf undivided or 2-lobed (rarely 4-lobed). Chatham Is. + South Is. (150–300 m) + North Is. (Waipoua area, 340–540 m) ..... *L. glaucescens* (p. 101)
   2. Plants green, yellow-green, brownish to dark brown, but without a dull, waxy, water-repellent surface 6
      6. Dorsal margin of leaves serrate or dentate-laciniate or ciliate 7
         7. Distal sector of leaf lobes ciliiform, ending in a uniseriate row of (5)8–15 distinctly elongated cells (3–4:1); lobe margins ciliate, often with paired cilia; leaves 2–2.2 mm wide × 1–1.2 mm long ..... *L. ulothrix* (p. 88)
         7. Distal sector of leaf lobes caudate to acute, the uniseriate row of 0–6 cells that are ± isodiametric or at most 2:1; lobe margins entire or with a few short teeth or spines; leaves at most 1.4 mm wide × 0.95 mm long 8
            8. Dorsal margin of disc and contiguous margin of lobe irregularly dentate to coarsely serrate; leaf lobes acute to short-acuminate; underleaves divided to at most 0.5 (the disc 12–16 cells high), the lobe margins entire or sparingly toothed; seta of 10–14 epidermal cell rows ..... *L. kirkii* (p. 82)

8. Dorsal margin of disc and confluent margin of lobe ± regularly spinose-dentate, with discrete, often curved, acuminate spines; leaf lobes caudate; underleaves divided to 0.55–0.8 (the disc 6–9 cells high), the lobe margins laciniate-multifid (rarely entire); seta of 9 epidermal cell rows ..... *L. hirta* (p. 85)

6. Dorsal margin of leaves entire (rarely with a basal tooth) 9

9. Leaf lobes setaceous, terminating in a uniseriate row of 6–10(12) elongated capillary cells. Leaf insertion distinctly incubous; trigones large and bulging to knotlike; underleaves distinctly connate on one side ..... *L. setigera* (p. 36)

9. Leaf lobes never setaceous, the lobes acute or terminating in a short uniseriate row of up to 2–5 cells 10

10. Leaves appressed to stem, distinctly ventrally secund, ± equally and shallowly (0.25–0.4) lobed, the two median lobes wider than the outer lobes. Slender, wiry plants with strongly ventrally secund branches ..... *L. procera* (p. 41)

10. Leaves spreading, not appressed to stem, the two median lobes not clearly wider than outer lobes. Leaves often asymmetrically lobed, the dorsal lobes often ± united in a perceptible pair, the ventral lobes usually shorter and often somewhat divergent from the dorsal pair 11

11. Leaves and underleaves variously appendaged, with accessory lobes and often lamellae; underleaves plicate, the lobes ventrally sulcate, the sinus bases strongly reflexed. Plants brown; branches spreading. Subalpine to alpine species ..... *L. ornata* (p. 49)

11. Leaves and underleaves not appendaged (rarely with marginal teeth); underleaves plane 12

12. Plants with brown pigments, typically erect, with distinctly ventrally secund branches (occasionally greenish with spreading branches in var. *parvula*). Disc cells often distinctly thick-walled, brownish; leaf and underleaf lobes often bluntly rounded. Seta with 16 rows of epidermal cell rows; capsule wall 4–5 stratose. Montane to alpine species ..... *L. obtusiloba* (p. 43)

12. Plants green, typically prostrate to procumbent, with spreading or ± decurved branches. Seta (where known) with 8 rows of epidermal cell rows; capsule wall (where known) 3-stratose 13

13. Median cells of leaf disc large (26–41 μm wide); plants medium-sized; underleaves inserted on 10 rows of stem cells; leaves 0.8–1 mm wide × 0.6–0.9 mm long. Leaves variable in shape, the ventral lobes typically not much shorter than the dorsal (the branch leaves ± equally 4-lobed). Cuticle of leaf disc smooth; median disc cells typically with trigones straight to large and bulging ..... *L. concinna* (p. 52)

13. Median cells of leaf disc smaller: 25 μm wide or less (exc. sometimes in *L. bidens*); plants small to minute; underleaves inserted on 9 or fewer rows of stem cells; leaves usually less than 0.5(0.6) mm in longest dimension 14

14. First branch underleaf consistently unlobed. South Is. (Westland Prov., 990 m) + North Is. (Rotorua area) 15

15. Leaves deeply (0.5–0.6) quadrifid, the lobes lanceolate; dorsal sinus descending at least 0.5 leaf length; lobes ending in ± elongated cells, the lobe cells mostly rectangulate; first branch underleaf subulate; stem half-leaf usually 0.45–0.55 bifid; branch leaves mostly 3-lobed ... *L. acantha* (p. 71)

15. Leaves less than 0.5 quadrifid, the lobes triangular, less than 3× as long as broad; dorsal sinus usually descending to 0.2–0.3; lobes ending in nonelongated cells, the lobe cells mostly

subquadrate; first branch underleaf ovate-lanceolate; stem half-leaf under 0.25 bifid; branch leaves 4-lobed .... *L. elobata* (p. 74)

14. First branch underleaf of mature shoots 2–4-lobed or mixed 1–2-lobed. Leaves mostly bisbifid: median sinus deeper, dorsal sinus usually shallow, usually strongly asymmetrical, the lobes always strongly unequal 16
    16. Leaves ± conspicuously papillose (at least on the lobes) or if indistinctly papillose (suboptimal populations of *L. laevifolia*) then the dorsal margin of disc ampliate and the outer wall of the marginal cells of disc and lobes not thickened 17
        17. Marginal cells of disc and lobes with free wall not differentially thickened; dorsal margin of disc ampliate, the margin cordate to auriculate at the insertion; leaves usually distinctly concave, wet or dry. Leaves coarsely papillose, the disc closely and distinctly striate-papillose; lobes with uniseriate row (when present) of nonelongated cells. Common; usually not below 300 m .... *L. laevifolia* (p. 56)
        17. Marginal cells of disc and lobes with a strongly thickened free wall (the wall often bulging into the cell lumen); dorsal margin of disc ± straight to moderately ampliate proximally, cordate at insertion, not clearly auriculate; leaves plane or only moderately concave, the lobes spreading or incurved. Rare or infrequent species 18
            18. Lobe tips caducous, the cells turgid, barrel-shaped, the septa constricted; lobes with uniseriate row of 2–4(5) cells, the cells ± isodiametric, the terminal cell rounded at the tip; median disc cells 17–24 μm wide; underleaves inserted on 7 rows of stem cells. Margins of disc and lobes occasionally toothed. South Is., 560–900 m ..... *L. fugax* (p. 63)
            18. Lobe tips not caducous, the cells with straight or concave walls, the septa dilated; lobes terminating in a single cell or at most 2 superposed cells, the cells elongated (to 2:1), the terminal cell ± tapering to a point; median disc cells 11–16 μm wide; underleaves inserted on 4–6 rows of stem cells. South Is. + North Is.; forest species .... *L. novae-zelandiae* (p. 66)
    16. Leaves smooth (rarely finely and indistinctly papillose); outer wall of marginal cells of disc and lobes distinctly thickened 19
        19. Plants medium-sized (the main shoots, 700–900 μm wide, leaf tip to leaf tip); underleaves inserted on 8 rows of stem cells; leaf disc 8–10 cells high at dorsal sinus, the cells ± longitudinally elongated; leaves with dorsal lobes ending in a uniseriate row of elongated (up to 2:1) cells. Plants of forests (sea level to 330 m on South Is.; to 920 m on North Is.) ..... *L. bidens* (p. 79)
        19. Plants minute to small (the shoots 365–490 μm wide, leaf tip to leaf tip); underleaves inserted on 5–6 rows of stem cells; leaf disc 9–12 cells high at dorsal sinus, the

cells quadrate or slightly longer than wide; dorsal lobes with cells of uniseriate row ± isodiametric or at most slightly longer than wide. Plants of forests + subalpine zone (570–1370 m); South Is. + North Is. .... *L. pumila* (p. 76)

1. Branching regularly and consistently twice-pinnate, the branches slender and drooping; leaves typically distant, vertically oriented, the insertion transverse. Plants erect, with rigid, woody stems 20
   20. Leaves inconspicuous, scalelike, narrower than stem, strongly erect and commonly ± appressed to stem, divided to 0.4–0.5 (median sinus) ..... *L. microphylla* (p. 28)
   20. Leaves conspicuous, wider than stem, stiffly patent or erect-patent from a spreading base, divided to 0.65–0.9 21
      21. Leaves ± symmetrical, lobes 6–8 cells wide at base, ending in a uniseriate row of 7–12 cells; dorsal margin of disc straight to slightly concave; underleaf disc 3–6 cells high, the lobes with a uniseriate row of 7–16 cells ..... *L. spinosissima* (p. 23)
      21. Leaves asymmetrical, lobes 14–24 cells wide at base, with a uniseriate row of 2–4(6) cells; dorsal margin of disc broadly ampliate; underleaf disc 14–24 or more cells high, the lobes with a uniseriate row of 1–3(4) cells ..... *L. pendulina* (p. 32)

Subg. *Dendrolepidozia* Schust.

Lepidozia subg. *Dendrolepidozia* Schust., J. Hattori Bot. Lab. 36: 386. 1973 (1972).

Plants usually stiffly erect, with a rigid, almost woody main axis with a thick-walled, polystratose cortex grading into the ± firm-walled medulla; plants usually a clear light to deep green, without brownish pigmentation of any sort. Shoot system usually repeatedly, copiously pinnate, sometimes with *Acromastigum*-type branches, with a regular, progressive diminution in vigor of both axes and appendages of the branches (the branch leaves typically smaller, more remote, often fewer-lobed), at least the ultimate branches often cernuous or drooping, often microphyllous and becoming flagelliform. Leaves usually remote, often strongly so, somewhat vertically oriented and only weakly to moderately incubously inserted, the stems extensively exposed both dorsally and ventrally; lateral leaves usually weakly asymmetrical, varying from handlike and deeply 4–5-parted to smaller, handlike to even scalelike, with abbreviated lobes. Underleaves similar in form to leaves, but somewhat smaller, 3–4-lobed with equal lobes, usually without rhizoids at their apices (rhizoids usually confined to tapered flagelliform axes or to lower portions of main stems).

TYPE—*Lepidozia spinosissima* Mitt.

Dendrolepidozia occurs usually in exceedingly deeply shaded sites in lowland forests and, as the name implies, the plants are strongly dendritic. Although leaf insertion is incubous, leaves are never incubously shingled. They are remote (on branches often exceedingly remote), and photosynthesis is, to a large extent, a function of the strongly chlorophyllose stems. The regular diminution in leaf size and complexity is marked (Fig. 8 : 3, 4, 10). Although terminal branches are usually of the *Frullania* type (Fig. 8 : 1, 2), in *L. spinosissima, Acromastigum*-type ventral terminal branches occur, with the half underleaf bifid rather than quadrifid (Schuster, 1982, fig. 1 : 2 and pp. 23–24).

In the freely 2–3-pinnate branching *L. spinosissima* is similar to *L. pendulina,* which we place within subg. *Notholepidozia,* in section *Pendulinae.* The two taxa also agree in the nearly vertical leaf orientation, the massive stems, and the mostly handlike leaves. *Lepidozia pendulina,* however, lacks *Acromastigum*-type branching (Fig. 10 : 1, 2), and has relatively strongly asymmetrical leaves with ampliate dorsal bases (Fig. 10 : 4) versus the weakly asymmetrical leaves with subequal lobes of *L. spinosissima* (Fig. 8 : 3, 4, 10). In *L. pendulina* stem half-leaves associated with terminal branches are nearly always bilobed (Fig. 10 : 2, 8, 12), while in *L. spinosissima* sporadic unlobed half-leaves may occur (Fig. 8 : 2). Basal branch underleaves in *L. pendulina* are (3)4-lobed (Fig. 10 : 1) versus 2–3(4)-lobed in *L. spinosissima* (Figs. 7 : 11; 8 : 1, 11). On balance, the strongly asymmetrical leaves of *L. pendulina* suggest that this species belongs in subg. *Notholepidozia* rather than in *Dendrolepidozia.*

Lepidozia spinosissima (Hook. f. & Tayl.) Mitt.
Figures 7 and 8

FIG. 7. *Lepidozia spinosissima* (Hook. f. & Tayl.) Mitt. **1.** Plant showing androecia on primary and secondary branches, the main axis with 9 androecia from ventral face of stem between arrows *a* and *b*, the plant also with a number of androecia (not shown) between the plant base and those drawn (these basal ♂ not included appear older, at times broken and presumably from a previous year's growth). **2.** Main shoot with androecium, ventral view (the leaf at lower left not shown); note also terminal branch and position of first branch underleaf. **3.** Antheridium. **4.**

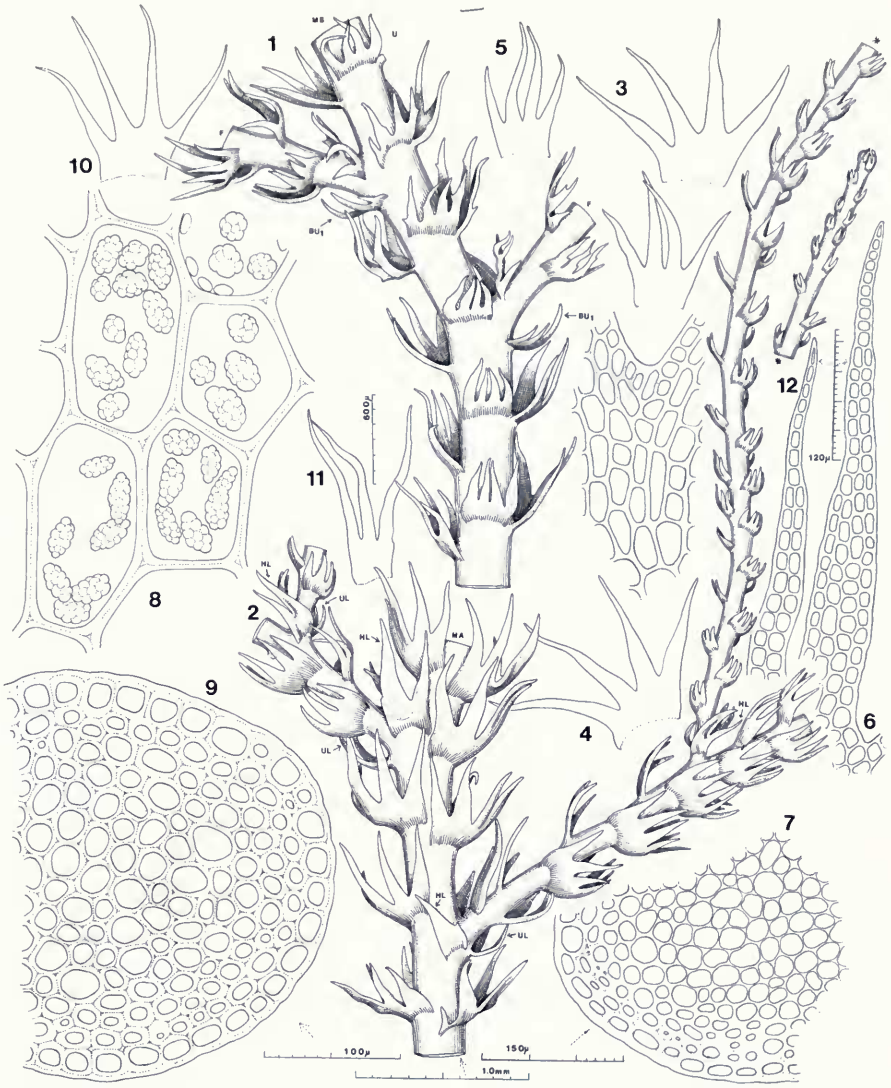

FIG. 8. *Lepidozia spinosissima* (Hook. f. & Tayl.) G. L. & N. **1.** Sector of upper part of main stem, ventral aspect, with two *Frullania*-type branches; at arrows, first branch underleaves (BUL) (×23; 1 mm scale). **2.** Sector of main axis, with primary and secondary branches (at upper right, continuation of the attenuate branch drawn to right; note dorsal half-leaves (HL) at arrows, and the primary branch underleaves (UL) (×23; 1 mm scale). **3.** Stem leaf and underleaves (×23; 1 mm scale). **4.** Stem leaf (×23; 1 mm scale). **5.** Stem underleaf (×23; 1 mm scale). **6.** Leaf lobe (×110; 120 μm scale). **7.** Stem cross section (×127; 150 μm scale). **8.** Lobe base cells with oil-bodies and (upper right) chloroplasts (× ca. 850). **9.** Main stem cross-section (×180; 100 μm scale). **10.** Leaf (×20; 600 μm scale). **11.** Underleaf (×20; 600 μm scale). **12.** Lobe apex (×110; 120 μm scale). (Figs. 1–2 from *Schuster 53380b*; 3–9 from *Schuster 67–244a*; 10–12, ex type.)

←

Portion of plant with perianth, ventral view; note primary and secondary terminal branches and the position of the first branch underleaves. **5.** Innermost bracts and bracteole. **6.** Bract lobes. **7.** Perianth, cross sections through median sector (*a*), distal 0.2 (*b*) and near apex (*c*). **8.** Portion of perianth mouth. **9.** Two leaves and (at right) an underleaf of main axis (DS = dorsal sinus). **10.** Half-leaf. **11.** First branch underleaves. (Figs. 1–3 from *Braggins 98/311,* New Zealand, North Is., North Auckland Prov., E edge of Waipoua Forest, Mataraurau Plateau; 4–8 from *Cameron 3797a,* New Zealand, South Auckland Prov., Coromandel Ranges, SW side of Maumaupaki, *Cameron 3797a*; 9–11, from *Engel 21109,* New Zealand, North Is., North Auckland Prov., SE corner of Waipoua Forest, just N of Tutamoe.)

Sendtnera spinosissima Hook. f. & Tayl. *in* Taylor, London J. Bot. 5: 373. 1846. *Lepidozia spinosissima* (Hook. f. & Tayl.) Mitt. *in* Hooker, Bot. Antarc. Voy. 2: 146. 1854. *Herbertia spinosissima* (Hook. f. & Tayl.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 397. 1877. Original material: New Zealand, *Edgerley* (*non vidi*).

Lepidozia longifissa Steph., Spec. Hep. 6: 364. 1922. Original material: New Zealand, *Zürn* (*non vidi*).

Plants erect, rigid, with somewhat ventrally secund spinescent branches, light green to yellow brown, highly nitid when dry, the shoots to 3.2 cm wide, including branches. Branching mostly of *Frullania* type, consistently bipinnate (rarely 3-pinnate), the primary branches each usually with 1–2 strong secondary branches arising near the base of the branch and positioned on the side of the branch toward the shoot apex, the secondary branches equal to or longer than primary branches; branches whiplike, occasionally becoming flagelliform, the leaves like those of main shoot except smaller; branch half-leaf 2-lobed or sporadically unlobed; first branch underleaf 2–3(4)-lobed, inserted on ventral-lateral side of main axis in similar plane to leaves of the main shoot, the branch appearing to originate in its axil. Primary branches with morphological ventral side oriented toward substrate. *Acromastigum*-type branches (?)occasional. Ventral-intercalary branching occasional. Stems rigid, ca. 16 cells in diameter, the cortical cells in 1 layer of somewhat elongated (at most 2–3× longer than wide and best viewed in longitudinal section) thick-walled cells; medullary cells longitudinally elongated, thick-walled, gradually becoming larger in diameter toward stem middle. Leaves rigid, plane or feebly concave, approximate, 0.7–1 mm long at longest point, 0.8–1.3(1.5) mm wide at widest point, stiffly patent, the insertion narrow, transverse; leaves slightly asymmetrical, subequally deeply 4(5)-lobed, divided to ca. 0.7–0.9, the lobes widely divergent, the distance from dorsal sinus base to insertion not much greater than that from ventral sinus to insertion, the sinuses gradually becoming deeper ventrally. Lobes narrowly and gradually attenuate, not noticeably in pairs, entire, 6–8(10) cells wide at base, terminating in a uniseriate row of (6)7–12 cells; cells of uniseriate row thick-walled, ± isodiametric to slightly longer than wide. Disc moderately asymmetrical, 7–9 cells high at dorsal sinus, 3–6 cells high at ventral sinus, the margins entire, the dorsal margin straight to slightly concave, the ventral shorter than the dorsal. Marginal cells of disc and lobes ± isodiametric, forming an indistinct border. Cells of disc middle thick-walled, trigones medium and straight-sided, occasionally with intermediate thickenings, isodiametric to longitudinally elongate along the lobe axis (the leaves thus subvittate), (15)18–27(32) × 26–35 μm; cuticle smooth. Oil-bodies colorless, 4–10(12) per cell, relatively large (3–5× chloroplasts in size), coarsely botryoidal, ovoid to ellipsoidal, sporadically subspherical. Underleaves widely spreading, symmetrically quadrifid to ca. 0.7–0.9, the lobes ± parallel to slightly divergent, filiform-attenuate, usually entire, rarely with a cilium toward base, terminating in a uniseriate row of 7–16 cells; disc 3–6 cells high at median sinus; disc margins entire. Underleaves indistinctly bordered like the leaves.

Androecia on inconspicuous, short, determinate, tightly spicate, cernuous, ventral-intercalary branches from main stem as well as primary and secondary branches, or terminating on such branches; bracts ventricose-cucullate, 2-lobed to ca. 0.3–0.5, the lobes apiculate to short acuminate, the lateral margin entire or on each with a tooth; antherida 1(2) per bract, the stalk 8–13 cells long, biseriate. Gynoecia rarely produced, on abbreviated ventral-intercalary branches issuing from main stem, with 1–2 ± mature gynoecia produced per shoot; bracts of innermost series much larger than leaves, erect and sheathing the perianth, the bracts deeply concave, narrowly ovate to subelliptical, shallowly and irregularly 3–4-lobed, the lobes acute to acuminate, composed of ± regularly rectangular and subrhomboidal cells, the apical end of the marginal cells often diverging and forming a crenulation or tooth, the lobe margins at times with a tooth composed of a uniseriate row of 2–3 cells, the lobe tips composed of a uniseriate row of 2 cells or a single cell or several laterally juxtaposed cells; lamina margins composed of narrowly elongate cells somewhat irregular in shape, the cells of median and basal portion of margin not projecting, the margin distally with cells often divergent and forming a crenulation and (sporadically) the margin with a few small teeth; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth narrowing toward the contracted, shallowly lobulate mouth, the mouth crenulate-denticulate, the teeth composed of a single cell or a uniseriate row of at most 3, thin to slightly thickened cells, the cells of the mouth finely striate papillose; perianth cells ± regularly long-subrect-

angular below mouth, the cells much thicker than those of the mouth and with a smooth cuticle; perianth (2)3-stratose near base.

Sporophyte not seen.

DIFFERENTIATION—*Lepidozia spinosissima* is one of the most distinctive New Zealand species of the genus. The erect, wiry, highly nitid (when dry) plants, with stiffly spreading, ventrally secund, spinescent branches, and the distant, rigid, stiffly patent, transversely inserted, deeply and symmetrically divided leaves are immediately recognizable.

DISTRIBUTION–ECOLOGY—Endemic to New Zealand (South Is., North Is.). A species of dense, wet, rich, low- to middle-elevation forests (typically sea level to 365 m). It typically occurs over decaying organic matter, such as on the forest floor among leaf litter and to a lesser extent on old logs. When terricolous, it occurs in particularly humid niches, such as damp hollows, stream banks, moist, shaded, humus-covered banks, and boggy areas. It also may occur as a component of dense bryophyte cover of vertical, dripping cliffs, such as those along the sea-level track to Bowen Falls at Milford Sound (*Engel 22010*), and may extend as high as 940 m on Mt. Te Aroha (North Is.), where it occurs on vertical cliff faces in a forest dominated by *Nothofagus menziesii* and *Griselinia littoralis* (*Engel 22130*).

SELECTED SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Doubtful Sound, *Simpson s. n.*—c. ♂ (F); Fiordland Natl. Park, Milford Sound, track to Bowen Falls, sea level, *Engel 22012* (F); ibid., Wilmot Pass, between Lake Manapouri and head of Doubtful Sound, *Barnard NZ-49* (F); ibid., Stuart Mts., W shore of Lake Thomson N of stream draining from Lake Wade, *Fife 7622* (F). OTAGO PROV.: Fiordland Natl. Park, near McKerrow Hut, head of Lake McKerrow, *Hatcher 1434* (F); just S of Haast Pass, 540–550 m, *Schuster 49648b* (F). WESTLAND PROV.: Cascade Road, Cascade ultramafic moraine, W of Martyr Saddle, SSW of Jackson Bay, ca. 30 m, *Engel 21777* (F); Jackson Bay, between confluence of Jackson River and Arawata River and Lake Ellery, off Jackson River Road, ca. 30 m, *Child H4255* as *L. microphylla* (F); Lake Ellery, ca. 30 m, *Child H4573* (F); Westland Natl. Park, along Gillespies Cook River Road, between Tornado Creek and Whelan Creek, *Engel 6595A* (F); near Hercules Creek on Route 6 in Mount Hercules Scenic Reserve, *Engel 6564A* (F); Arthur's Pass Natl. Park, Otira River gorge, W of Arthur's Pass, ca. 300–365 m, *Schuster 48488c* (F); ca. 12 mi N of Greymouth, *Moore 85* as *Lepidozia gottscheana* (CHR). NELSON PROV.: Southern end of Heaphy Track, between summit of saddle beside Kohaihai Bluff and footbridge over Kohaihai River, less than 120 m, *Fife 7084* (F); Paparoa Natl. Park, Bullock Creek Road, along Bullock Creek, NE of Punakaiki, ca. 25 m, *Engel 21591* (F); N bank of Fox River, ca. 1.5 km E of Route 6, less than 30 m, *Fife 4968* (F); Stony Creek, E of Westport, ca. 150 m, *Child H3549* as *L. microphylla* (F); valley of the Oparawa River, on track between logging road bridge at mouth of Narya Creek and Moria Gate Limestone Arch, 215 m, *Fife 7049*. NORTH ISLAND. WELLINGTON PROV.: Akatarawa, 820 m, *Braggins 84/412A*—c. per. (AKU); ibid., Waterfall Creek near Bullstream, E of Akatarawa summit, 335 m, *Braggins 84/367A* (AKU); Tararua Range, Puffer to Smiths Creek track, *Moss s.n.* (AKU). TARANAKI PROV.: Pukeiti Bush, near New Plymouth, *Hatcher 404* (F). SOUTH AUCKLAND PROV.: Mt. Te Aroha, ca. 3 km E of Te Aroha, 900–940 m, *Engel 22130* (F); Coromandel State Forest Park, ridge between Webb Creek Track and Billy Goat Track, 510–540 m, *Engel 22330* (F); ibid., summit of Table Mt., 835 m, *Engel 22384* (F); Coromandel Ranges, Kauaeranga Valley, Waiora Stream Valley, ca. 200 m, *Cameron 2852* (AKU); Coromandel Ranges, SW side of Maumaupaki (Camels Back), ca. 800 m, *Cameron 3797a* (AKU). NORTH AUCKLAND PROV.: NE Waitakere Ranges, Spraggs Bush, ca. 360 m, *Engel 22191* (F); West Auckland Waitakere Ranges, Fairy Falls Track, ca. 320 m, *Braggins 92/48c* (AKU); Kaihu Forest, headwaters of Opouteke Stream, *Bellingham* (AKU); SE corner of Waipoua Forest, just N of Tutamoe, 540 m, *Engel 21109* (F); Mangamuka Gorge, 245 m, *Braggins 84/312* (AKU).

Subg. *Mastigolepidozia* Schust.

Lepidozia subg. *Mastigolepidozia* Schust., Beih. Nova Hedwigia 118: 187. 2000.

Plants stiffly erect, at maturity 2–3-pinnate usually, with drooping, progressively and conspicuously smaller, often distally attenuate branches; vegetative branching uniformly of *Frullania* type, remote. Stem of main axes woody, rigid, 22–25 cells in diameter, with a very weakly distinct hyaloderm; 2–3(4) intracortical strata smaller-celled, firm-walled, grading into the somewhat larger-celled, less firm-walled medulla. Leaves of stems and branches exceedingly remote, scalelike, broad-based, only weakly incubous, suberect, appressed or weakly spreading from stem; leaves of main axes asymmetrical (ventral lobe smaller, shorter), usually less than 0.45 quadrilobed, the lobes and disc edentate; leaves of branches progressively smaller, 3–4-lobed, narrower and less asymmetrical. Leaf cells firm-walled, with 2–5 rather large, finely botryoidal oil-bodies. Underleaves of main stems exceedingly remote, mostly broader than long, quadrilobed.

TYPE—*Lepidozia microphylla* (Hook.) Lindenb.

Including perhaps no more than 4–5 species of almost exclusively austral range. Only *L. porto-*

ricensis Fulf., which we have not studied, occurs in the Antilles.

It is uncertain whether the few species belong in one or two sections. The only regional species belongs in sect. *Microphyllae*. Our single species is similar to *L. subdichotoma* Spruce (Trans. Proc. Bot. Soc. Edinburgh 15: 361. 1885) of Ecuador in that, even though primary branches lie mostly at an acute angle to the main axis (Fig. 9 : 1), the primary branches typically are almost dichotomously furcate and both secondary and tertiary branches are greatly reduced in vigor compared to the main axis. The pseudodichotomous branching of primary branches is highly distinctive. Perianths in this group are very large for the overall plant size.

Sect. *Microphyllae* (Lindenb.) Grolle

Sect. *Microphyllae* (Lindenb.) Grolle, Feddes Repert. 87: 269. 1976.
Lepidozia I. *Microphyllae* Lindenb. *in* G. L. & N., Syn. Hep. 201. 1845. Lectotype (*fide* Grolle, 1976): *Lepidozia microphylla* (Hook.) Lindenb.

Lepidozia microphylla (Hook.) Lindenb. Figures 6 : 10–13; 9

Jungermannia microphylla Hook., Musci Exot. 1: *pl. 80, f. 1–6.* 1818. *Mastigophora microphylla* (Hook.) Mont. *in* d'Orbigny, Voy. Amér. Mér. 7, Bot. 2: 73. 1839. *Lepidozia microphylla* (Hook.) Lindenb. *in* G. L. & N., Syn Hep. 202. 1845. Original material: New Zealand, South Is., Dusky Bay, *Menzies* (*non vidi*).
Lepidozia multipinna Steph., Spec. Hep. 3: 591. 1909. Original material: New Zealand, *Dall* (*non vidi*).

Plants erect, rigid, distinctly wirelike, delicate in appearance, with drooping, ventrally secund branches, the branch axils (in field) with prominent, glistening droplets of water, the plants pale green (± strawlike color or whitish in herb); the shoots to 4.5 cm wide, including branches. Branching mostly of *Frullania* type, consistently bipinnate (occasionally 3-pinnate), the primary branches each usually with 2–4 strong secondary branches arising near the base of the branch and positioned on the side of the branch toward the shoot apex, the secondary branches equal to or longer than primary branches; branches whiplike, filiform-attenuate, the leaves scalelike, obliquely spreading, approximate; branch half-leaf often caducous; first branch underleaf 2–4-lobed, inserted on main axis in similar plane to leaves of main shoot, the branch appearing to originate in its axil; primary branches with morphological ventral side oriented toward substrate. Ventral-intercalary branching occasional. Stems fleshy, rather brittle, ca. 24 cells in diameter, the cortical cells in a distinct layer of isodiametric to slightly elongated cells (best viewed in longitudinal section), larger in diameter than subepidermal cells; medullary cells thick-walled, the outer several rows with walls thicker than the median core cells. Leaves inconspicuous, scalelike, narrower than the stem, slightly concave, markedly distant, (340) 385–420(450) μm long at longest point, (340) 380–450(490) μm wide at widest point, strongly erect, commonly ± appressed to stem, occasionally feebly spreading, the insertion transverse to weakly incubous; leaves asymmetrical, unequally 4-lobed, divided to ca. 0.4–0.5 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion, the sinuses gradually becoming deeper ventrally. Lobes acuminate, not noticeably in pairs, entire, 4–5 cells wide at base, terminating in a uniseriate row of 2-4(5) cells; cells of uniseriate row ± isodiametric, thick-walled; cuticle as in disc. Disc asymmetrical, 7–9 cells high at dorsal sinus, 3–5 cells high at ventral sinus, the margins entire, the dorsal margin straight to slightly curved, the ventral shorter than the dorsal. Marginal cells of disc ± isodiametric, forming an indistinct border. Cells of disc middle thick-walled, ± isodiametric, 24–31 μm wide and long; cuticle faintly striate-papillose. Oil-bodies 2–5 per median cell, finely botryoidal and almost granular in aspect (the spherules small), the oil-bodies relatively large for cell size, 3.5 × 6.5 to, more usually, 4.5–5 × 9–11 up to 5 × 7–8 μm. Underleaves minute, widely spreading, symmetrically quadrifid to ca. 0.3–0.4, the lobes abbreviated, only 3–5 cells long; disc 3–4(5) cells high at median sinus; disc margins entire.

Plants dioecious. Androecia[10] on inconspicuous, short, determinate, tightly spicate, straight, ventral-intercalary branches from primary or secondary branches; bracts ventricose-cucullate, 2-lobed to ca. 0.3–0.4, the lobes acute to apiculate to short acuminate, the lateral margins entire or on each side with a small to large tooth, the margins often also with a few slime papillae; antheridia 1 per bract, the stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series much

[10] Some populations have nematode galls at the tips of flagelliform branches; these should not be confused with androecia (see comments under *L. pendulina*).

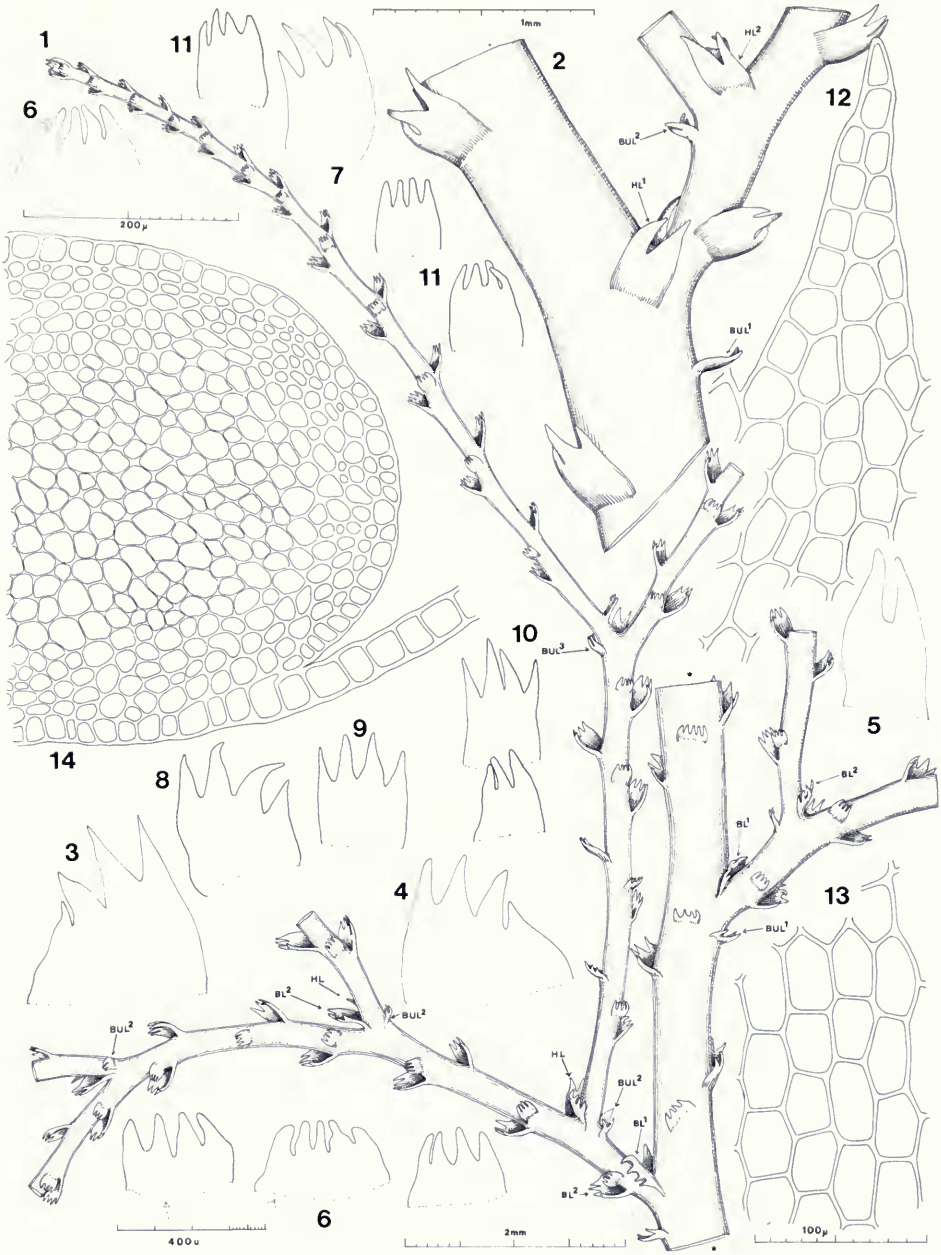

FIG. 9. *Lepidozia microphylla* (Hook.) Lindenb. **1.** Part of erect, leafy axis, ventral aspect; at asterisks sector of main axis; at left, part of the branching system (BL^1 and BL^2), near base, first two lateral primary branch leaves; distally, BUL^2 = primary appendages, underleaves, of secondary branches and BL^2 = primary lateral leaf of secondary branch; at HL portions of the half-leaves associated with *Frullania*-type branches visible; on right-hand side, primary branch underleaf (BUL^1) and primary branch leaf (BL^1), as well as secondary branch primary leaf (BL^2) labeled; above primary appendage, an underleaf (BUL^3) of tertiary branch labeled (×14.5; 2 mm scale). **2.** Small sector of main axis and bases of primary and secondary branches, dorsal aspect; stem half-leaf = HL^1, half-leaf of primary branch = HL^2, first branch underleaf of primary branch = BUL^1, of secondary branch, BUL^2 (×29; 1 mm scale). **3–4.** Stem leaves (×50; 400 μm scale). **5.** Stem half-leaf, associated with branch (×50; 400 μm scale). **6.** Stem underleaves (×50; 400 μm scale). **7–8.** Leaves from primary branches (×50; 400-μm scale). **9.** Underleaf, primary branch (×50; 400 μm scale). **10.** Leaf from secondary branch (above) and first branch underleaf from secondary branch (below) (×50; 400 μm scale). **11.** Underleaves from secondary branches (×50; 400 μm scale). **12.** Lobe of stem leaf (×230; 100 μm scale). **13.** Dorsal cortical cells of stem (×230; 100 μm scale). **14.** Stem cross section (×142; 200 μm scale). (All from *Schuster 85-2719.*)

larger than leaves, erect and sheathing the perianth, the bracts deeply concave to canaliculate, narrowly ovate; apices with 4 short, irregular lobes composed of irregularly sinuate-rhomboidal cells that at their apical end are laterally free for varying lengths, the lobes crenate-denticulate to ciliate; lamina composed of ± regularly subrectangular cells, the submarginal cells rhomboidal, the margin bordered by elongate, thin-walled, sinuate-rhomboidal cells that at their apical end occasionally diverge to form a projection, the margin irregularly crenate-denticulate to the base, the teeth at most of 3 superposed cells; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, terete below, obscurely trigonous above, distinctly 3-plicate toward mouth, the perianth gradually narrowing toward the contracted, shallowly 3-lobed mouth, the lobes composed of irregularly sinuate-rhomboidal cells that at the apical end are laterally free for varying lengths, the lobes crenate-denticulate to ciliate; perianth cells ± regularly subrectangular below mouth; perianth 2–3 stratose near base.

Capsule oblong, the wall 54–60 μm thick, of 4–5 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheetlike thickenings and several small nodules alternating with walls that are devoid of thickenings (or are sporadically locally thickened), the transverse walls usually devoid of thickenings or sporadically with an isolated nodule; innermost layer of cells with ± tiered, narrowly rectangular, with semiannular bands common, rather wide, close and numerous, usually complete, rarely forked.

Spores 10.1–11.9 μm, exine pale brown, thin, with low, rather coarse, close papillae and short-vermiculate markings. Elaters rigid, nontortuous, 11–14.9 μm wide, only slightly tapering toward tips, bispiral, the spirals 3.4–4.8 μm wide.

DIFFERENTIATION—*Lepidozia microphylla* is immediately recognizable by the erect, fleshy, pale yellow green shoots with rigid, distinctly wirelike, drooping, ventrally secund branches. The shoots are rather brittle when dry. The leaves are inconspicuous, distant and scalelike, nearly appressed to and narrower than the stem, and almost transversely inserted (Fig. 9 : 1, 2). A distinctive field character of the species is the presence of tiny, glistening water droplets in the branch axils.

A notable feature of this species is the "low" insertion of the basal branch underleaf of primary branches: this structure, usually trifid, superficially appears to be inserted on the stem rather than the branch base (Fig. 9 : 1, 2).

Although *L. microphylla* and its immediate allies of the Neotropics are very distinct plants vegetatively, the gynoecium—in particular the ♀ bracts—is very similar to what is seen in ordinary taxa of subg. *Lepidozia* and *Notholepidozia*.

Lepidozia microphylla is apt to be confused in the field with *L. spinosissima* owing to the stiffly erect growth, the copious branching, and the pale yellowish color. Both taxa tend to occur in large, often pure swards, are ± similar in size, with the well-separated individual plants having a dendritic aspect.

The leaf of *L. microphylla* is similar to that of the otherwise very different *L. pendulina* in being strongly asymetrically 4-lobed (Fig. 9 : 3, 4). The leaf, however, is much smaller, averaging 385–415 μm broad × 385–410 μm long. The ventral lobe is shaped much like the others and is not set off as a narrow "finger." The distal portions of the leaf are distinctly smaller-celled; cells are ca. (20)23–25 × 24–32 μm versus 33–37 × 44–52 μm in a small basal region. Median cells (Fig. 6 : 10) have a conspicuous middle lamella, are evenly thick-walled, and have mostly 2–5 oil-bodies each. The oil-bodies are clearly less coarsely botryoidal—almost granular-botryoidal—than in *L. pendulina* and *L. concinna* (compare Fig. 6 : 1, 5) and, in median cells, range from 3.5 × 6.5 to 4.5–5 × 9–11 μm, or 5 × 7 μm.

Underleaves are distinctive in being broader than long, rather shallowly 4-lobed, with narrow lobes, unusual in the relatively conspicuous and persistent apical slime papilla (Fig. 6 : 11).

The stem (Fig. 9 : 14) has a rather well-defined hyaloderm, surrounding a layer 1–2(3) strata thick of somewhat smaller, very thick-walled cells that gradually grade into a firm-walled medulla.

DISTRIBUTION–ECOLOGY—Endemic to New Zealand (South Is., North Is.). A species of dense, wet, rich, lower-elevation forests (sea level to 340 m). It typically occurs on the forest floor, where it may form extensive, dense carpets. It is a locally common floor plant at some sites, such as rich mixed *Nothofagus* forests or kakikatea swamps, and often occurs in boggy, seepage niches. To a lesser extent it may also be found on old logs or tree bases (such as of kauri).

SELECTED SPECIMENS SEEN—NEW ZEALAND: SOUTH ISLAND: SOUTHLAND PROV.: Lake Hauroko, ca. 215 m, *Child 1538* (F); Doubtful Sound, *Simpson s. n.* (F); Fiordland Natl. Park, Tutoko River, W of

Milford Sound, 50 m, *Engel 18820* (F). WESTLAND PROV.: Cascade Road, just W of Jackson River, ca. 8–12 km SW of confluence of Jackson and Arawata Rivers, 25–90 m, *Engel 22970* (F); Lake Ellery, *Child H4571* (F); between confluence of Jackson River and Arawata River and Lake Ellery, off Jackson River Road, sea level, *Engel 17913*—c. ♂ + sporo. (F); Haast, 3 mi. N of bridge, ca. 15 m, *Child H702* (F); Lake Matheson, sea level, *Child H371* (F); Westland Natl. Park, along Gillespies Cook River Road, between Tornado Creek and Whelan Creek, *Engel 6578A* (F); Gillespies Beach Road, 12 km W of Fox Glacier, ca. 150 m, *Child H4849*—c. ♂ + sporo. (F); Mahinapua, S of Hokitika, ca. 60 m, *Child H3668* (F). NELSON/WESTLAND PROV. BOUNDARY: Porarari River Gorge, junction of Porarari River Gorge, junction of Porarari River Track and the Inland Pack Track, ca. 30 m, *Fife 4850* (F). NELSON PROV.: Little Wanganui, W coast, ca. 15 m, *Child 416* (F); valley of the Oparara River, 0.5 km S of Moria Gate Limestone Arch, 226 m, *Fife 7073* (F); Paparoa Natl. Park, Inland Pack Track, SW of terminus of Bullock Creek Road, NE of Punakaiki, ca. 35 m, *Engel 21675* (F); swamp at N end of Lake Hanlan and gorge of stream draining lake and entering Tidal Creek between lake and State Highway 67, 30–90 m, *Fife 7142* (F). NORTH ISLAND: NORTH AUCKLAND PROV.: Waipoua Forest, track to Te Matua Ngahere, ca. 340 m, *Engel 22561* (F); SE corner of Waipoua Forest, just N of Tutamoe, *Engel 21086* (F); same loc., *Braggins 94/246*—c. sporo. (AKU); Omahuta Forest Kauri Sanctuary, E of Mangamuka Bridge, 260 m, *Engel 21001*—c. per. (F).

Subg. *Notholepidozia* Schust., subg. nov.

Subgeneri Lepidoziae similis sed corporibus oleosis distincte vel grosse botryoideis, inflorescentiis uniformiter dioicis, axe e cellulis intracorticeis rigidis atque parietibus firmis vel percrassis composito differt.

TYPE—*Lepidozia novae-zelandiae* Steph.

Plants typically creeping to ascending, often loosely procumbent, occasionally erect, light yellowish or even whitish green, ranging to olive to brownish, but never glaucous, the cells lacking a waxy cuticle. Branching 1(2)-pinnate (consistently bipinnate only in *L. pendulina*), often regularly so, the branches often running out into flagellae; lateral branching always *Frullania* type; ventral-intercalary vegetative branches usually few or none, but ♂ and ♀ branches normally from axils of underleaves of leading stems or primary branches. Stems not woody (exc. *L. setigera*), mostly with a 1-stratose cortex of larger cells (at times verging on an indistinct hyaloderm) which have only moderately thickened or almost thin walls; medullary cells smaller, often thick-walled. Leaves remote to imbricate, typically strongly incubously inserted and oriented (exc. *L. pendulina*), often handlike, distally decurved, strongly (infrequently weakly) asymmetrically (3)4(5)-lobed; leaves with both disc and lobes usually asymmetrical, the dorsal sectors larger and longer, the dorsal margin longer, usually more convex (sometimes strongly ampliate); leaves usually 0.3–0.5 lobed, with narrowly triangular to longly acuminate lobes, the lobe (and disc) margins entire or toothed with coarse, broad-based, teeth which are never opposed in pairs. Cells of leaves usually firm-walled, often quite thick-walled and with lumina rounded at the angles, less often with distinct trigones. Oil-bodies in distal and median cells usually 2–5 per cell, finely to coarsely botryoidal. Underleaves smaller than lateral leaves, usually 3–4-lobed.

Subgenus *Notholepidozia* is very well represented in New Zealand and is strongly polytypic there. Species occur from sea level well into the alpine region, where they occur mostly on soil in clefts between ledges or crevices in cliff faces, but also sometimes in moory areas or in snow-tussock grasslands. The species usually grow procumbent when not crowded and almost never occur stiffly erect as do the taxa of subg. *Dendrolepidozia*. Most of the species are easily known by their predominantly 4-lobed, almost handlike, asymmetrical leaves, with larger dorsal lobes.

We have, with some reluctance, concluded that the Austral taxa here placed into *Notholepidozia* must be segregated as an autonomous subgenus from subg. *Lepidozia*, as typified by *L. reptans*. All of the taxa of *Notholepidozia* that we have seen have distinctly botryoidal oil-bodies (Figs. 31 : 11, *L. kirkii*; 6 : 1, 2, *L. pendulina*; 6 : 5, 6, *L. concinna*), while *L. reptans* and two other Northern Hemisphere species have small, homogeneous oil-bodies (cf. fig. 86 : 6, Schuster, 1969). *Lepidozia reptans* has a relatively simple axial anatomy, with a leptodermous medulla; it is autoecious. All of the Austral species we have studied from living plants consistently have botryoidal oil-bodies, have a stem with a firm-walled or rigid medulla, and are unisexual.

Lepidozia reptans in many respects is not typical of the genus; it is a pity that it is the generic type because it is a thoroughly "strange" element within *Lepidozia*. Oil-bodies in *L. reptans* are small, smooth, and numerous, occurring (8)10–16(25) per cell versus the botryoidal oil-bodies, often larger, found usually (1)2–8 per median cell in *Notholepidozia*. In the botryoidal oil-bodies *Notholepidozia* is similar to the two Austral subgenera, *Dendrolepidozia* (cf. Fig. 8 : 8, *L. spinos-*

issima) and *Austrolepidozia* (cf. Fig. 6 : 10, *L. microphylla*). This suggests that botryoidal oil-bodies are part of the original genetic "equipment" of the genus as a whole and that *L. reptans* represents, geographically and cytologically, an isolated extreme within the genus as a whole.

Lepidozia reptans is, as far as known, wholly Laurasian in range. Early reports (from Java, Juan Fernandez, Hawaii, South America; Frye & Clark, 1937–47) are all erroneous (Schuster, 1969, p. 25). The report of the species from as far south as Colombia and Venezuela (Fulford, 1966) is almost surely incorrect; pl. 40 : 5 in Fulford (l.c.) illustrates a plant with a high disc and short lobes, whereas *L. reptans s. str.* has a lower and more asymmetrical disc (cf. fig. 86 : 3, 4, Schuster l.c.).

Sect. *Pendulinae* Schust.

Lepidozia sect. *Pendulinae* Schust., Beih. Nova Hedwigia 118: 197. 2000.

Plants firm, erect, vigorous, 2(3)-pinnate, the branches drooping, ventrally secund, freely becoming flagelliform. Basal branch underleaf inserted at branch base, usually deeply quadrifid. Stem woody, with up to (5)6–7(8) thick-walled strata of relatively small cells, the outer layer not or hardly distinguishable from the inner ones; medulla larger-celled, the cells rather thin-walled. Leaves asymmetrical, almost transversely inserted, concave, quadrifid, the two dorsal lobes larger, separated by a shallower sinus; ventral lobes narrower, lanceolate, separated from the dorsal two by a deeper sinus.

TYPE—*Lepidozia pendulina* (Hook.) Lindenb.

Including a single regional species. When well-developed, the freely bipinnate, sporadically tripinnate, tapered, and ventrally secund branching separates the species from any other regional taxon of subg. *Notholepidozia.* Branching is suggestive of *Dendrolepidozia,* but the total lack of *Acromastigum*-type branches separates *L. pendulina* from *L.* (*D.*) *spinossissima.* On well-developed plants, branches, apices of uppermost branches, and the shoot tip are diagnostically ventrally strongly secund or even coiled, unlike in *L. spinosissima.* The sporadic ventral branches in *L. pendulina* are all intercalary and axillary.

The strongly asymmetrical leaves of *L. pendulina* consist of two similar dorsal lobes that are separated by a relatively shallow sinus; the dorsal pair of lobes is separated by a deeper sinus from the two narrow, lanceolate, longly tapered ventral lobes. Ventral lobes typically are separated from each other by a very deep sinus that often descends for 0.75–0.85 the leaf length (cf. Fig. 10 : 3, 4). Cells in *L. pendulina* at leaf bases may have as many as 16–20 oil-bodies (Fig. 6 : 2).

Lepidozia pendulina (Hook.) Lindenb. Figures 6 : 1–3, 8, 9; 10

Jungermannia pendulina Hook., Musci Exot. 1: *pl. 60, f. 1–5.* 1818. *Lepidozia cupressina* var. *τ pendulina* (Hook.) Lehm. & Lindenb. *in* Lehmann, Nov. Min. Cogn. Stirp. Pug. 4: 39. 1832. *Lepidozia pendulina* (Hook.) Lindenb. *in* G. L. & N., Syn. Hep. 208. 1845. *Mastigophora pendulina* (Hook.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. Original material: New Zealand, South Is., Dusky Bay, 1791, *Menzies* (*non vidi*).
Lepidozia gigantea Steph., Spec. Hep. 3: 600. 1909. Original material: New Zealand, *Doll* (*non vidi*).

Plants erect, rigid, with ventrally secund branches, pale green, the shoots robust, to 6 cm wide, including branches. Branching mostly of *Frullania* type, consistently bipinnate (rarely 3-pinnate), the primary branches each usually with 1–2 strong secondary branches arising near the base of the branch and positioned on the side of the branch toward the shoot apex, the opposing side of the primary branch with 0–2(3) branches, the secondary branches equal to or longer than primary branches; branches whiplike, often becoming flagelliform, the leaves like those of main shoot except smaller; branch half-leaf 2-lobed or sporadically unlobed; first branch underleaf (3)4-lobed, inserted on ventral-lateral side of main axis in a plane similar to leaves of main shoot, the branch appearing to originate in its axil; primary branches in suberect to erect plants with morphological ventral side oriented toward substrate. Ventral-intercalary branching rare and sporadic. Stems rigid, ca. 30 cells in diameter, the cortical cells in 1 layer of isodiametric, firm-walled cells (best viewed in longitudinal section), internal to the epidermal layer are 2–3 to 4–6 rows of thick-walled, longitudinally elongated cells; central portion of stem made up of cells larger in diameter and with thin walls. Leaves rigid, slightly concave, distant, 1.1–1.4 mm long at longest point, (1.7)1.9–2.5 mm wide at widest point, stiffly patent, the insertion transverse; leaves asymmetrical, unequally 4(6)-lobed, the leaves divided to ca. 0.65–0.75 (median sinus), the distance from dorsal sinus base to insertion much greater than that from ventral sinus to insertion. Lobes broadly at-

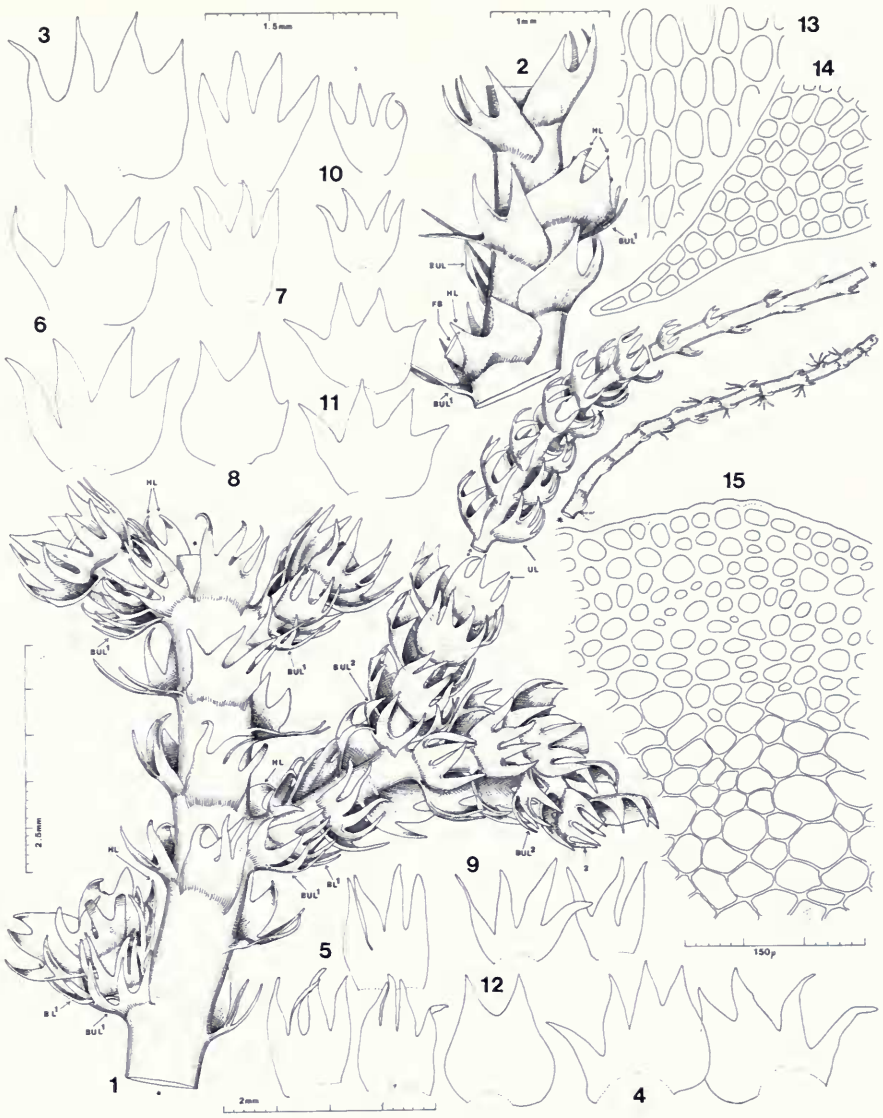

FIG. 10. *Lepidozia pendulina* (Hook.) Lindenb. **1.** Part of plant, ventral view; main axis at asterisks; at BUL[1] the primary appendages, underleaves, of primary branches; at BL[1] primary lateral leaves of branches; at BUL[2] primary underleaf of secondary branch, and distal to it (at 3) succeeding branch underleaf; at HL, stem half-leaves; the secondary branch at upper right with sector removed (arrows), the branch so curved that underleaves (UL) are not perfectly aligned; at asterisks, the distal sectors join together (×12; 2.5 mm scale). **2.** Small sector of main axis, dorsal aspect; two *Frullania*-type branch bases (FB), with the bifid half-leaves (HL) and primary branch appendages (BUL[1]) labeled. Note the juxtaposition (upper branch base) of half-leaf and primary branch underleaf, so that the branch superficially appears to arise in an axillary position. At SUL the stem underleaf visible, in part; note the subtransverse insertion of dorsal halves of leaves (×15.5; 1 mm scale). **3.** Stem leaf (×17; 1.5 mm scale). **4.** Stem leaves (×14; 2 mm scale). **5.** Stem underleaves (×14; 2 mm scale). **6.** Leaves of primary branches (×17; 1.5-mm scale). **7.** Underleaves, primary branch (×17; 1.5 mm scale). **8.** Stem half-leaf, primary branch (×17; 1.5-mm scale). **9.** Initial branch underleaves from primary branches (BUL[1] in Figs. 1–2), showing variation in lobe number (×14; 2 mm scale). **10–11.** Appendages from secondary branches; above, two underleaves; below, two leaves (×17; 1.5 mm scale). **12.** Half-leaf of stem (×14; 2 mm scale). **13.** Dorsal cortical cells (×160; 150 μm scale). **14.** Cells of leaf lobe (×160; 150 μm scale). **15.** Sector of stem cross section (×160; 150 μm scale). (All from *Schuster 67-400,* New Zealand, Fiordland, Falls Creek.)

tenuate (the dorsal lobes acute, the ventral lobe more narrowly attenuate and curved), widely divergent, the dorsal pair of lobes partially united, the others distinct and spreading, the ventral lobe often widely divergent as a "claw," the dorsal lobes entire, (10)14–24 cells wide at base, the lobes terminating in a uniseriate row of 2–4(6) cells (6–7 in ventralmost lobe); cells of uniseriate row ± isodiametric to slightly longer than wide, thick-walled. Disc distinctly asymmetrical, 20–30 cells high at dorsal sinus, 12–18 cells high at ventral sinus, the margins entire, the dorsal margin broadly ampliate, the ventral much shorter than the dorsal, slightly curved. Cells of disc middle thick-walled, trigones medium and straight-sided, occasionally with intermediate thickenings, ± isodiametric to elongate, 18–26(29) × 24–33(42) μm, in ± regular longitudinal files; median basal cells enlarged, in 1–2 rows, with walls often nodulose; cuticle smooth to indistinctly striate. Oil-bodies in median cells (2)3–8, locally to 10–14 per cell, rather coarsely botryoidal, spherical to ovoid, 4 × 4–5 μm to 4–4.5 × 5–7 μm, sporadically 3.6 × 4.5 μm; basal cells locally large and 40–42 × 50–59 μm and with 16–20 oil-bodies each, coarsely segmented, 5–7 μm to 5.5 × 10 μm. Underleaves often weakly to distinctly plicate, widely spreading, symmetrically 4(6)-fid to ca. 0.65–0.7 (median sinus), the sinus bases somewhat reflexed, the lobes ± parallel, somewhat ventrally sulcate, narrowly and gradually attenuate, entire, terminating in a uniseriate row of 1–3(4) cells; disc 14–24(32) cells high at median sinus, the margins reflexed, entire or sporadically with a tooth.

Plants dioecious. Androecia[11] on inconspicuous, short, determinate, tightly spicate, cernuous ventral-intercalary branches from main shoot and primary + secondary branches (in flagelliform or leafy sectors); bracts ventricose-cucullate, 2-lobed to ca. 0.3, the lobes acute to short acuminate, the lateral margin with several slime papillae; antheridia 2 per bract, the stalk biseriate. Gynoecia only sporadicaly produced, on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series much larger than leaves, erect and sheathing the perianth, the bracts deeply concave, broad ovate-subrectangular; apices with 4–5 short, ± regular lobes composed of ± regularly rectangular and (especially at the lobe extremities) irregularly sinuate-rhomboidal cells, the apical end of the marginal cells often thickened and feebly diverging and forming a crenulation, the lobes thus finely crenulate; lamina composed of ± regularly subrectangular to prosenchymatous cells, the margin bordered by thin-walled cells of variable shape and orientation, the cells often ± sinuate-rhomboidal, the apical or free end of marginal cells variously divergent and forming a short projection or a tooth, the margin irregular and crenulate to crenate-denticulate, the margins occasionally with a ciliiform-laciniiform process; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth, the lobe margins composed of irregularly sinuate-rhomboidal cells that, at the apical end, project for varying lengths; mouth cells laterally free for varying lengths and only rarely completely free laterally, the mouth thus crenate-denticulate; perianth cells ± regularly subrectangular to feebly prosenchymatous below mouth, and here the cuticle is obscurely striate; perianth 3–4 stratose near base.

Seta with 16 rows of outer cells surrounding an inner core of numerous much smaller cells. Mature capsules not seen.

DIFFERENTIATION—Well-developed plants of this species are not likely to be confused with any other New Zealand member of the genus on general aspect alone. However, small, poorly developed populations are often difficult to recognize. Such plants are compact, with secondary branches weakly developed or absent, and have imbricate leaves. In these cases the broad, transversely inserted, entire-margined leaves (at least near the base of best-developed shoots), the narrow median disc cells, and the large underleaves with ± parallel, ventrally sulcate lobes will generally distinguish this species. Absence of pigments and the lack of underleaf armature will aid in distinguishing the species from *L. obtusiloba*. *Lepidozia concinna* is sometimes suggestive of a diminutive *L. pendulina* in the shape of its leaves and under-

[11] Some populations have nematode galls at the tips of primary and secondary branches. These are conspicuous, budlike, and spherical, with several nematodes in each swelling. The nematodes considerably alter the morphology of the leaves to structures that are in ca. 2–3 pairs, cucullate, 4-lobed to ca. 0.2–0.3 and with lobes acute to short acuminate. The budlike swellings should not be confused with androecia. Nematode galls occur in a variety of Hepaticae but heretofore are unknown for Lepidoziaceae (cf. also Schuster, 1966).

leaves (as, for example, in the type of *L. latiloba* Col.) but typically has at least a moderately incubous leaf insertion, much larger median disc cells, and dorsal lobes that are at most 9 cells wide at the base.

The leaf areolation of *L. pendulina* is distinctive: The leaf cells are thick-walled, arranged in ± regular longitudinal files, and appear small and narrow in proportion to the size of the leaf, giving the leaf a densely cellular appearance, even under the dissecting microscope.

Vigorous plants of *L. pendulina* may have very rigid main stems, with 6–8 outer cell layers forming, collectively, a rigid cortex (Fig. 10 : 15). Although the main shoots are moderately anisophyllous, at least the secondary branches may become virtually isophyllous (Fig. 10 : 1).

DISTRIBUTION–ECOLOGY—New Zealand (South Is., North Is.), Tasmania, Australia (Victoria).

The species occurs in dense, very wet forests over a broad altitudinal gradient but is more typical of middle- to upper-elevation sites. For example, it may occur at the upper limits of *Nothofagus menziesii* forests (stations at ca. 900 m on South Is. and ca. 1180 m on North Is.), as well as in subalpine *Nothofagus solandri* forests with *Phyllocladus alpinus, Senecio bennettii, Pseudopanax* spp., *Dracophyllum traversii,* and *Coprosma* (915 m, *Fife 8005*). In the southern sectors of South Is, it may occur in forests at lower elevations, including at sea level. For example, it is found on the sides of bryophyte-covered logs in the rich mixed *Nothofagus* forest with tree fern understory along the Tutoko River at 50 m in Fiordland.

The species typically occurs over organic substrates such as the forest floor (particularly in damp leaf litter), where it may form extensive, at times pure, carpets; it may be associated with *Trichocolea mollissima, Plagiochila suborbiculata, P. gigantea, Schistochila nobilis,* and *Bazzania nitida,* among others. It also occurs on damp, bryophyte-covered banks and wet, bryophyte-covered, rotted logs. The species often is a component of the flora of sites where the floor, boulders, and trees are densely covered with bryophytes. At the upper forest limits smaller phases of the species may form extensive pure populations on rotted, decorticated wood (Moraine Creek Track, *Engel 23218*) or on old tree stumps (Punekiri Bluff, *Engel 23321*).

SELECTED SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Lake Hauroko, ca. 215–305 m, *Child H1547, H1591* (F); Fiordland Natl. Park, Expectation Stream, *Zotov s. n.* (F); ibid., Stillwater River, *Zotov s. n.* (F); ibid., Stuart Mts., W shore of Lake Thomson N of stream draining from Lake Wade, 300 m, *Fife 7722* (F); immediately N of Ten Mile Bush, near W shore of Lake Te Anau and ca. 20 km N of town of Te Anau, 200 m, *Engel 23203* (F); Fiordland Natl. Park, off track along East Branch of Eglinton River, SE of Mt. Eglinton and NNE of Te Anau, 440 m, *Engel 18773*—c. ♂ (F); ibid., Cascade Creek, near Lake Gunn, tributary of Eglinton River, ca. 365 m, *Child H2591* (F); ibid., Moraine Creek Track, area N of Moraine Creek, W of Hollyford River, 610 m, *Engel 23218* (F); ibid., Moraine creek, Hollyford Valley, ca. 120–200 m, *Schuster 48111* (F); ibid., Tutoko River, W of Milford Sound, 50 m, *Engel 18813* (F). OTAGO PROV.: Fiordland Natl. Park, track along Falls Creek, near junction of Hollyford River road and road to Milford Sound, *Schuster 67–406a* (F); Route Burn Valley, ca. 520 m, *Child 2460* (F); Sylvan Lake, Dart River, ca. 365 m, *Child H1167* (F); Beans Burn, tributary of Dart River, 455 m, *Child 1267* (F); Fiordland Natl. Park, trail between Gunn's Hut and Hidden Falls, ca. 30 mi SE of Lake McKerrow, *Hatcher 696* (F); ibid., head of Lake McKerrow, *Hatcher 1338* (F); ibid., N of McKerrow River, Martins Bay, *Hatcher 749* (F); ibid., Martins Bay, *Hatcher 1375A* (F). OTAGO/WESTLAND PROV. BOUNDARY: Summit area of Haast Pass, 570 m, *Engel 17963*—c. ♂ (F); Haast Pass watershed, ca. 455 m, *Child s.n. 48* (F). WESTLAND PROV.: Cascade Road, just NE of Martyr Saddle and immediately N of Jackson River, ca. 20 m, *Engel 21835A* (F); ibid., just W of Jackson River, ca. 8–12 km SW of confluence of Jackson and Arawata Rivers, 25–90 m, *Engel 22994* (F); S facing upper reaches of Haast River, ca. 0.6 miles N of Haast Pass, ca. 520 m, *Schuster 59616a* (F); Mt. Aspiring Natl. Park, Cross Creek, 1.1 km N of Haast Pass, 540 m, *Engel 21881* (F); ibid., Blue River near confluence with Makarora River, NNE of Makarora, 310 m, *Engel 18912* (F); ibid., off track to Mt. Brewster, below and W of Mt. Armstrong, SW of Mt. Brewster, ca. 900 m, *Engel 17842* (F); Lake Ellery, ca. 60 m, *Child H4574* (F); between confluence of Jackson River and Arawata River and Lake Ellery, off Jackson River Road, sea level, *Engel 17915* (F); near Fox Glacier, *Mrs. Knight* (F); N side of Waiho River, within 0.8 mi. of jct. with Callery River, ca. 2–3.5 mi. below Franz Josef Glacier, 75–250 m, *Schuster 59729a* (F); Arthur's Pass Natl. Park, N of Kellys Creek near Hwy 73, above campground, 420–475 m, *Engel 18353*—c. ♂ (F); Otira, track to Mt. Barron, *Whitehouse 29641* (F); Camp Creek, W of Alexander Range, 510–1040 m, *Reif C63D, C216C* (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Bealey Valley Track, ca. 875–900 m, *Engel 22854* (F). CANTERBURY PROV.: Arthur's Pass Natl. Park, near Bealey Glacier Vista, *Engel 6839* (F); ibid., S bank of upper reaches of Bealey River near Bealey Track (to Bealey Glacier), within 1.5 km NW of Jack's Hut, 875–950 m, *Fife 6145* (F); Margaret's Tarn (Bealey Glacier Track), 915 m, *Fife 8005* (F); Arthur's Pass vicinity, 1/4 mile W of Bealey Valley, *Whitehouse 29585* (F). NELSON/WESTLAND PROV. BOUNDARY: Porarari River Track, 4 km from road, at junction with Bullock Creek Track, ca. 150 m, *Child H4978* (F). NELSON: Mt. Sewell, Paparoa Range, ca. 915 m, *Child*

H2783 (F); Paparoa Mts., cirque on E flank of Mt. Priestly, 960 m, *Fife 5573* (F). NORTH ISLAND: WELLINGTON PROV.: Erua (South of National Park), Erua Forest 2 km from State Highway 4, *Braggins 92/129* (F); Tongariro Natl. Park, ca. 8 km from Ohakune on Ohakune Mt. Road, ca. 950 m, *Engel 21334*—c. ♂ (F); Tongariro Forest, Okupata Caves site, ca. 600 m, *Braggins 92/136* (F). NEAR GISBORNE/SOUTH AUCKLAND PROV. BOUNDARY: Urewera Natl. Park, track to Whakataka Hut from Lake Waikaremoana, N of western extremity of Lake Waikaremoana, 1000–1100 m, *Engel 23311* (F). GISBORNE PROV.: Urewera Natl. Park, Panekiri Range, summit area of Pukenui in vicinity of Punekiri Bluff, 1180 m, *Engel 23321* (F); ibid., Huiarau Range, summit area of Te Rangaakapua, 1265–1320 m, *Engel 23409* (F).

Sect. *Setigerae* Schust.

Lepidozia sect. *Setigerae* Schust., Beih. Nova Hedwigia 118: 193. 2000.

Plants closely 1-, sporadically 1(2)-pinnate, erect or suberect, pale yellowish or whitish green, vigorous. Stems rigid, with a hyaloderm moderately distinct, the 2–3 cell layers within firm-walled, grading into the medulla, which is less strongly thick-walled (in section often strongly thickened only at the angles). Leaves strongly incubous, imbricate, strongly asymmetric, 4(5) lobed (dorsal two lobes shorter, separated by a shallower sinus than ventral 2–3 lobes), with strongly ampliate dorsal margin, and a short, non-ampliate ventral margin; lobes acuminate, ending in up to 6–10(12) superposed, elongated cells. Underleaves often connate on one side, cuneate-based, obtrapezoidal, 4–6-lobed, the lobes acuminate and setigerous like the leaf lobes.

Gynoecial bracts in 3–4 progressively larger series, at least 0.5 quadrifid into narrow, erect, gradually tapered lobes that end in ca. 9–13 superposed single cells.

TYPE—*Lepidozia setigera* Steph.

Monotypic. Without close allies. In dorsal aspect the leaves appear conspicuously imbricate on account of the broadly overlapping ampliate dorsal margin of the disc (Fig. 11 : 1). On main shoots the stem is wholly hidden in dorsal aspect. Both leaves and underleaves may show elaboration of a strong accessory lacinium, so that seemingly 5-lobed leaves (Fig. 11 : 3, 4) and 5–6-lobed underleaves (Fig. 11 : 5, 6) frequently occur. Basal branch underleaves are oriented in line with stem lateral leaves and the branches superficially seem to originate in their axils (Fig. 11 : 2). The first branch underleaves are large, often trifid, at times with one lobe seemingly again bifid, or bearing a strong cilium (Fig. 11 : 7).

Lepidozia setigera is a strikingly isolated species. Unlike ordinary species of the genus, which have shallowly lobulate bract apices, it has the bracts basically deeply incised, for at least 0.5 their length, into narrowly lanceolate-caudate lobes that end in setae formed of 9–13 cells. (Fig. 12 : 12).

Lepidozia setigera Steph. Figures 11 and 12.

Lepidozia setigera Steph., Spec. Hep. 3: 599. 1909. Original material: New Zealand, South Is., *Kirk* (*non vidi*).

Plants suberect, somewhat flexuous, with ventrally secund branches, pale green, the shoots robust, to 3 cm wide, including branches. Branching mostly of *Frullania* type, closely and regularly pinnate, the primary branches often very long, becoming whiplike and flagelliform, the primary branches occasionally developing into new leading shoots; secondary branches occasionally present, 1(2) per primary branch; branch half-leaf ± symmetrical, broadly ovate, 2-lobed to ca. 0.5, entire; first branch underleaf 3–4-lobed, with a few marginal cilia, inserted on lateral side of stem immediately below branch base and aligned with leaves of main shoot, the branch appearing to originate in its axil; second and subsequent branch underleaves ventral-lateral in position and gradually becoming morphologically ventral. Ventral-intercalary branching sporadic, stoloniform or leafy and developing into a new leading shoot. Stems stiff and woody, ca. 24 cells in diameter, the cortical cells in 1 layer of thin-walled cells distinctly larger than medullary cells (up to 2× larger); medullary cells moderately thickened, the outer several rows with walls thicker than the median core cells. Leaves rigid, slightly concave, the lobes in same plane as lamina and not incurved, strongly imbricate and completely hiding stem in dorsal view, 1.5–1.7 mm long at longest point, 2–2.4 mm wide at widest point, patent, the insertion distinctly incubous and somewhat recurved at dorsal end; leaves distinctly asymmetrical, unequally 4(5)-lobed, the leaves divided to ca. 0.5–0.6 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion, the sinuses ± U-shaped, gradually becoming deeper ventrally. Lobes subulate, the lobes somewhat divergent, not noticeably in pairs, the ventral lobe often spreading as a "claw," the

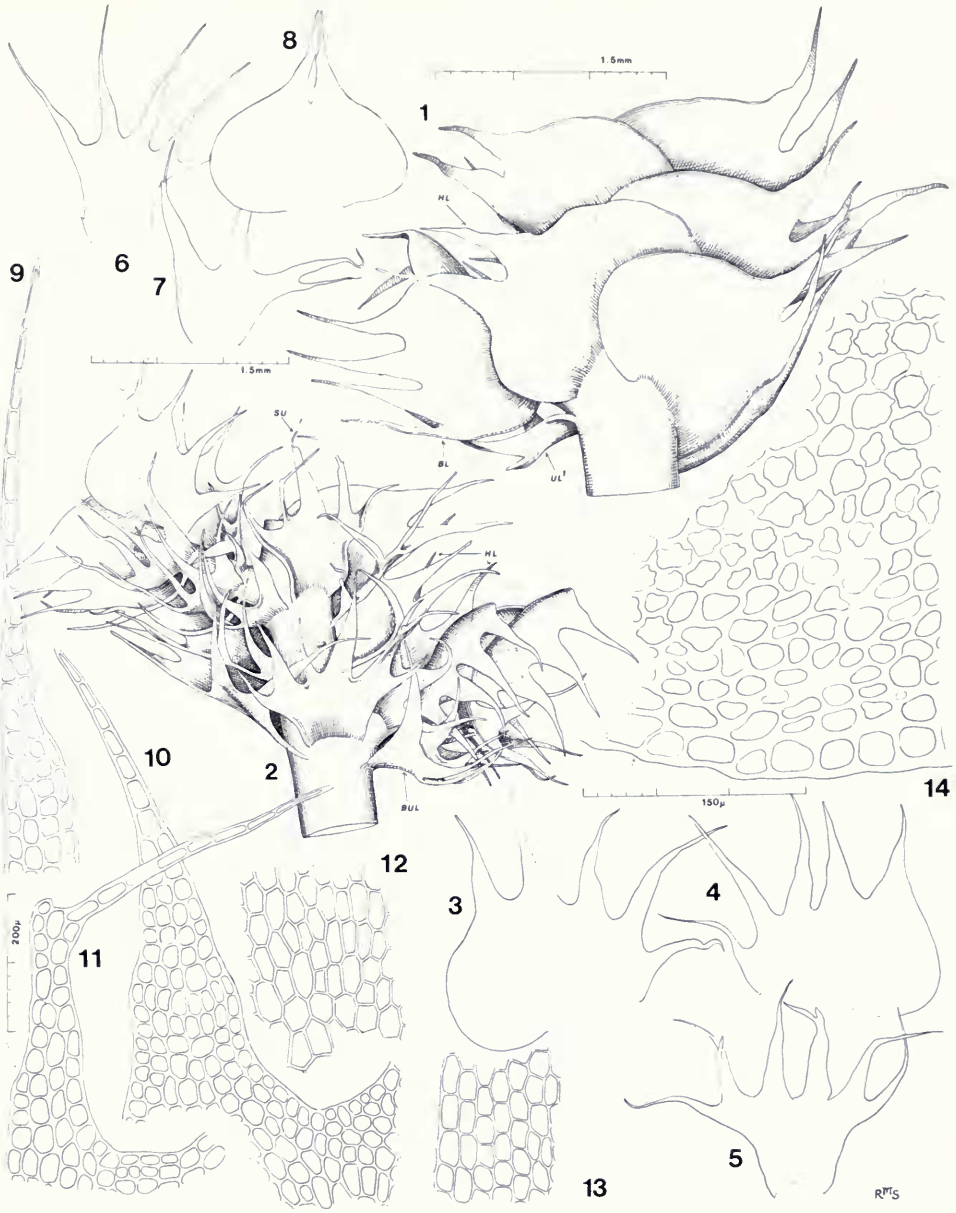

FIG. 11. *Lepidozia setigera* Steph. **1.** Shoot sector, main axis, with base of lateral branch at left, dorsal view. At HL the stem half-leaf; at UL^1 the primary branch underleaf, trifid in form; at BL the branch leaf (×20; 1.5 mm scale, adjacent). **2.** Shoot sector, ventral aspect. At SU, stem underleaf; at BUL^1, the trifid primary branch underleaf, the branch superficially axillary in it; at HL, the stem half-leaf (×17.5; 1.5 mm scale, adjacent). **3–5.** Two stem leaves and an underleaf (×17.5; lower 1.5 mm scale). **6.** Branch underleaf (×17.5; lower 1.5 mm scale). **7.** First branch underleaf (×17.5; lower 1.5-mm scale). **8.** Half-leaf associated with *Frullania*-type branch (×17.5; lower 1.5 mm scale). **9, 11.** Underleaf lobes (×90; 200 μm scale). **10.** Dorsal lobe at sinus, stem leaf; note small cells in sinus (×90; 200-μm scale). **12, 13.** Basal and median leaf cells, respectively (×90; 200 μm scale). **14.** Part of stem cross section (×198; 150 μm scale). (All from *Schuster 67-400,* New Zealand.)

FIG. 12. *Lepidozia setigera* Steph. **1.** Median leaf cells (×220; 100 μm scale at right). **2.** Foot and seta base, excised sporophyte (×25; 700 μm scale). **3.** ♀ Bracts + bracteole, innermost series (×17.5; left 1.5 mm scale). **4.** ♀ Bract, second series (×17.5; left 1.5 mm scale). **5.** ♀ Bract, outermost series (×17.5; left 1.5 mm scale). **6.** Perianth-bearing ventral-intercalary branch (×22; lower 1.5 mm scale). **7.** Stem leaf (×17.5; left 1.5 mm scale). **8.** Stem underleaf (×17.5; left 1.5 mm scale). **9.** Stem half-leaf (×17.5; left 1.5 mm scale). **10.** Stem half-leaf (×17.5; left 1.5 mm scale). **11.** Cross section, immature seta (×110; 200 μm scale). **12.** Apex of lobe of ♀ bract (×185; 150 μm scale). (All from *Schuster 95-750,* New Zealand, North Is.)

lobes entire, the dorsal lobes 8–11 cells wide at base, terminating in a uniseriate row of 6–10(12) cells (the ventral often somewhat longer); cells of uniseriate row, often hyaline, tapering, with ± swollen dilated septa, 2–5:1, thick-walled, becoming longer and narrower toward the tip and capillary, the terminal cells finely tapering, 8–10:1, the cuticle finely striate-papillose. Disc distinctly asymmetrical primarily because of strong dilation of dorsal sector, the dilated portion up to ca. 0.5 the disc area, the disc (18)20–25 cells high at dorsal sinus, 12–16 cells high at ventral sinus; dorsal margin distinctly and broadly ampliate, entire; ventral margin much shorter than the dorsal, entire or sometimes with a process. Cells of disc middle thin-walled, trigones large and bulging to knotlike, 26–33 × 34–52 μm; median basal cells larger; cuticle smooth to indistinctly striate-papillose. Underleaves often distinctly connate on one side (the connation to 7–8 cells high) spreading, concave, imbricate, symmetrically 4-fid to ca. 0.5–0.6 (median sinus), the sinus bases somewhat reflexed, the lobes plane or reflexed, diverging, filiform-attenuate from a narrow base and ultimately with a long-ciliiform tip, entire or with a ciliiform spine, the lobes appearing to terminate in a blunt tip, the lobe continuing as a subapical, often abaxially oriented, ciliiform process with a uniseriate row of 8–13 cells; disc 18–22 cells high at median sinus, the disc margins somewhat reflexed, on each side often with a ciliiform process distally, the underleaves then appearing 6-lobed.

Androecia not seen. Gynoecia rarely produced, on abbreviated ventral-intercalary branches issuing from main stem, solitary or with up to 6 mature gynoecia produced per shoot, the base of gynoecium bulbous and rhizoidous; bracts of innermost series much larger than leaves, erect and sheathing the perianth, the bracts deeply concave, broadly ovate to suborbicular from a narrow base, 4(6)-lobed to ca. 0.5–0.6, the lobes caudate, the setaceous tips, composed of a uniseriate row of 6–10 thick-walled, elongate cells, the cells immediately basal to the uniseriate row elongate and at times subsigmoid, the lobes entire or armed with a few short to long basal cilia; lamina margins armed with spinose teeth and straight to contorted cilia; bracteole similar in size and form; gynoecium with a few scales within or immediately exterior to innermost bracts, the scales armed with contorted cilia. Perianth long and prominent, slenderly cylindrical-fusiform, terete below, obscurely trigonous in distal 0.25–0.4, distinctly and deeply triplicate toward mouth, the perianth gradually narrowing toward the strongly contracted, contorted mouth, the contracted sector membraneous and, with emergence of the capsule, splitting into 4–6 narrowly long-attenuate lobes, the contracted sector composed of elongate, narrow, thick-walled, slightly sinuate cells; mouth cells 4–9:1, laterally fused for varying lengths and thickened at the summit, the mouth thus rather regularly crenulate to crenate-denticulate; perianth cells ± regularly subrectangular below contracted sector and here the cuticle is inconspicuously striolate; perianth 3–5 stratose near base.

Seta with 12–13 rows of large outer cells surrounding an inner core of ca. 40–50 small cells. Capsule wall 52–54 μm thick, of 5–6 layers; outer layer of cells with two-phase development, the longitudinal walls very thin, with sinuous, sheetlike swellings (very narrow for valve size) and a few nodulelike swellings alternating with walls that are devoid of thickenings, the transverse walls usually devoid of thickenings or sporadically have an isolated sheetlike thickening; innermost and each of intermediate layers subequal in thickness, the innermost layer of cells ± tiered, narrowly rectangular, semiannular bands common, narrow, close and numerous, sporadically incomplete, rarely forked.

Spores 11–12.5 μm, exine brown, thin, with dense, close papillae and short vermiculate markings. Elaters rigid, nontortuous, 15.8–16.8 μm wide, slightly tapering toward tips, bispiral, the spirals 4.8–5.3 μm wide.

DIFFERENTIATION—This is one of the easiest of our species to identify. The lobes of both leaves and underleaves are setaceous at their apices, terminating in a uniseriate row of greatly elongated cells (Fig. 11 : 9). Unlike *L. ulothrix,* which also has lobes terminating in a uniseriate row of elongated cells, this species has disc and lobe margins that are uniformly entire (Fig. 11 :3, 4). Also notable is the broad and marked ampliation of the dorsal sector of the leaf, the dilated portion up to half the disc area.

Lepidozia setigera has distinctive gynoecia. There are 3–4 gyres of gradually larger, imbricate bracts. Those of the outer series are about 0.6–0.7 quadrifid, with tapered, acuminate, distally setigerous lobes that are entire or occasionally bear a single basal cilium (Fig. 12 : 4, 5). Disk margins are sparingly short ciliate, often with recurved cilia. Innermost bracts are much larger (Fig. 12 : 3) but similarly quadrifid, with acuminate-caudate long, tapered lobes ending in 9–13 or more firm-

walled, elongated single cells (Fig. 12 : 12). Disk margins are sparingly ciliate, the short cilia often reflexed. Perianths are 2–3-layered to at least the basal third but unistratose above; the narrow mouth is crenulate to crenate-denticulate.

DISTRIBUTION–ECOLOGY—Endemic to New Zealand (South Is., North Is.). The species occurs sporadically in lower- to middle-elevation forests (60–150 m on South Is., 260–340 m on North Is.), where it is terricolous or found on old, humus-covered logs, at times mixed with *Bazzania adnexa.* On North Is. it chiefly occurs in kauri forests. It is rather common in the Waipoua Forest Reserve on relatively well-insulated peaty ground under, for example, old *Leptospermum* or on very rotted, bryophyte-covered shaded logs in *Agathis* forest containing *Dacrydium* and other podocarps.

SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. WESTLAND PROV.: Ahaura, ENE of Greymouth, ca. 150 m, *Child H3770* (F); Mahinapua, S of Hokitika, ca. 60 m, *Child H3666* (F); 2 km N of White Horse Creek, ca. 305 m, *Child H5430* (F). NORTH ISLAND. NORTH AUCKLAND PROV.: Waipoua, track to Mahuta, ca. 305 m, *Child H2151* (F); Waipoua Forest, Track to Te Matua Ngahere, ca. 340 m, *Braggins 92/149* (F—c. sporo.); same loc., *Engel 22563* (F); ibid., Yakas Track, *Braggins 94/214* (AKU); Omahuta Forest Kauri Sanctuary, E of Mangamuka Bridge, 260 m, *Engel 20993* (F), *Schuster 95-750*—c. per.

Sect. *Notholepidozia*

Notholepidozia, as here circumscribed, may still be heterogeneous. Sporophyte and gynoecium features of *L. obtusiloba* are different from other members of the section. That species has a seta consisting of 18 outer rows (Fig. 16 : 2), whereas other members of the section for which the seta is known have only 8 outer rows (Fig. 20 : 12, *L. laevifolia*). The capsule wall of *L. obtusiloba* is 4–5-stratose (Fig. 16 : 3), whereas other members of the section have a 3-stratose capsule, where known. There appears to be at least a weak correlation between gametophytic vigor and seta and capsule anatomy (see Taxonomic Characters and Morphology, p. 18). This correlation should be tested by the study of sporophytes of those species heretofore known to lack them. Further subdivision of sect. *Notholepidozia* may be necessary after obtaining sporophyte data of *L. ornata* (a relatively large species), *L. concinna* (a median-sized species) and those of more of the smaller taxa (*L. novae-zelandiae* and *L. bidens*). The perianth mouth of *L. obtusiloba* also differs. Mouth cells of this species are laterally fused to the summit or nearly so, and the mouth is thus merely regularly crenulate (Fig. 15 : 6, 7), versus mouth cells that are laterally free for varying lengths at the apical end, resulting in a crenate-denticulate mouth in all other species of the section for which perianths are known.

Section *Notholepidozia* has undergone extensive, in part seemingly recent, speciation in New Zealand. Species limits, therefore, are at times difficult to draw. Nonetheless, several characters are of particular taxonomic value within the section. The width of the ventral merophytes (on well-developed main stems) is often helpful, particularly among the complex of species that includes *L. novae-zelandiae* (4–6 cells wide; Fig. 24 : 14), *L. laevifolia* (6–8 cells wide; Fig. 20 : 11), *L. bidens* (8 cells wide; Fig. 30 : 10) and *L. concinna* (10 cells wide; Fig. 18 : 11) (see discussion on p. 15).

The form of the basal branch underleaf is sometimes useful and seems fixed in both *L. acantha* and *L. elobata,* where it is nearly uniformly unlobed (cf. Figs. 27 : 3, 5; 28 : 1, 2). The remainder of our species of sect. *Notholepidozia* have the basal branch underleaf 2–3- or 3–4- or, in several cases, 2–4-lobed. Moreover, in several species (e.g., *L. laevifolia, L. pumila*) unlobed basal branch underleaves also may be present, though exceptionally. The plasticity of the character in the section renders it of minimal taxonomic use, aside from the unlobed species (see also the discussion on p. 14).

The degree of leaf cell papillosity varies considerably within the section from weak and delicate to rather coarse, and may be subject to some environmental influence. Nevertheless, the character is valuable within the section (see discussion on p. 16).

Leaf shape, in general, shows sufficient intraspecific variation that it is difficult to use taxonomically. In general, the two dorsal lobes form a pair, separated by a shallower sinus than that which separates them from the two ventral lobes. The many figures illustrate the variation seen; it may be as great intraspecifically as between species. Some taxa have a relatively shallow dorsal sinus (Fig. 28: 3, 4, 7–9, *L. elobata*), usually less than 0.3 the leaf length; others have it deeper and narrower (Fig. 25 : 1, 2, 5, 11, *L. novae-zelandiae*), but intrapopulational variation is sufficiently extensive as to largely bridge such differences.

Species differences are occasionally difficult to draw in this section, in part because of intrapopulational malleability. It is therefore essential

that several shoots be studied for assessment of taxonomic characters.

Lepidozia procera Mitt. Figure 13.

Lepidozia procera Mitt. *in* Hooker, Bot. Antarc. Voy. 3: 231. *pl. 180, f. 1.* 1859. Original material: Tasmania, without specific locality, *Gunn*; Mt. Wellington, *Oldfield* (*non vidi*).
Lepidozia breviloba Steph., Spec. Hep. 3: 596. 1909. Original material: New Zealand, Great Barrier Is., *Kirk* (*non vidi*).

Plants erect, slender and wiry, with strongly ventrally secund branches that are often oriented parallel to one another, pale green, the shoots to 1.5 cm wide (stem to branch extremities). Branching nearly exclusively of *Frullania* type, closely and regularly pinnate, the primary branches becoming distinctly whiplike, long-flagelliform, microphyllous and rhizoidous, the nonmicrophyllous leaves ± symmetrically 4-lobed, the primary branches occasionally developing into new leading shoots; secondry branches rare, 1–2 per primary branch; branch half-leaf ± symmetrical, narrowly ovate, shallowly bilobed; first branch underleaf (2)3–4-lobed, inserted on ventral-lateral side of junction of main axis and branch and aligned with branch underleaves. Ventral-intercalary branching sporadic, leafy. Stems stiff, 14–16 cells in diameter, the cortical cells in 1 layer of somewhat thick-walled cells somewhat larger than the medullary cells (the cortical cells well-defined in longisection); 1–2 subepidermal layers with walls thicker than both epidermis and internal medullary cells, the medullary cells toward stem middle thick-walled and with trigonelike thickenings. Leaves appressed to stem at least in basal sector, somewhat concave, contiguous to weakly imbricate, 0.35–0.5 mm long and wide at longest and widest points, suberect, ventrally secund particularly when dry, the insertion weakly to distinctly incubous; leaves slightly to rather markedly asymmetrical, ± equally or, more often, unequally 4-lobed, divided to ca. 0.3–0.45 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion (often markedly so). Lobes parallel to slightly divergent, short-attenuate to acute, entire, the 2 median lobes wider and often slightly longer than the outer lobes, 5–7 cells wide at base; lobes terminating in a single cell or a uniseriate row of 2–3(4) cells, the cells of uniseriate row ± isodiametric, thick-walled and with the septa distinctly thickened and swollen; cuticle of lobes smooth to indistinctly and obscurely papillose. Disc moderately to distinctly asymmetrical, subquadrate to deltoid, 17–26 cells high at dorsal sinus, 10–16 cells high at ventral sinus, the margins entire but the septa of marginal cells distinctly thickened and swollen, the dorsal margin slightly to moderately ampliate and broadly curved, the ventral straight or slightly curved (often with a slight dilation at base), shorter than the dorsal. Cells of disc middle evenly thick-walled, 10–13 × 13–19 μm, in ± regular longitudinal files; median basal cells larger (up to 2× diameter of cells of second row), in one row; cuticle of disc smooth. Underleaves often narrowly connate on one side, small, ca. 0.7–0.9× the stem width, ± appressed to slightly spreading, quadrate, symmetrically quadrifid to ca. 0.3–0.4, the lobes abbreviated, only (4)5–6(8) cells long; disc (5)7–9 cells high at median sinus; disc margins entire.

Androecia and gynoecia not seen.

DIFFERENTIATION—The superficial aspect of plants of this species is that of a miniature *L. spinosissima,* both taxa being slender and wiry, with the branches having a spinescent appearance (in the case of *L. procera* due to the ventrally secund leaves; Fig. 13 : 1, 4). The primary branches of *L. procera* are noteworthy in being strongly ventrally secund and often oriented parallel to one another (Fig. 13 : 1, 14).

The leaves are closely appressed to the stem (Fig. 13 : 1, 4) and, coupled with being ventrally secund, lend the shoots and branches a markedly smooth aspect dorsally. The leaves are shallowly lobed, the two median lobes larger and somewhat longer than the outer lobes (Fig. 13 : 5–7). The orientation of leaf lobes is thus distinctive among New Zealand species (with the exception of *L. spinosissima*), which for the most part have a tendency for the dorsal lobes to be paired to united and the ventral pair of lobes smaller and somewhat divergent. Also distinctive is the broadly curved dorsal margin of the leaf, which is longer than the slightly curved or straight ventral margin; the difference in margin lengths is related to the (often marked) greater distance between dorsal sinus base to the leaf insertion than from ventral sinus base to insertion (Fig. 13 : 5–7). The leaf areolation is distinctive. Disc cells are evenly very thick-walled, and the cells are in longitudinal files (Fig. 13 : 9). The septa of marginal cells, especially those of the dorsal margin, are distinctly thickened and swollen (Fig. 13 : 11). This character is not always fully expressed in suboptimal

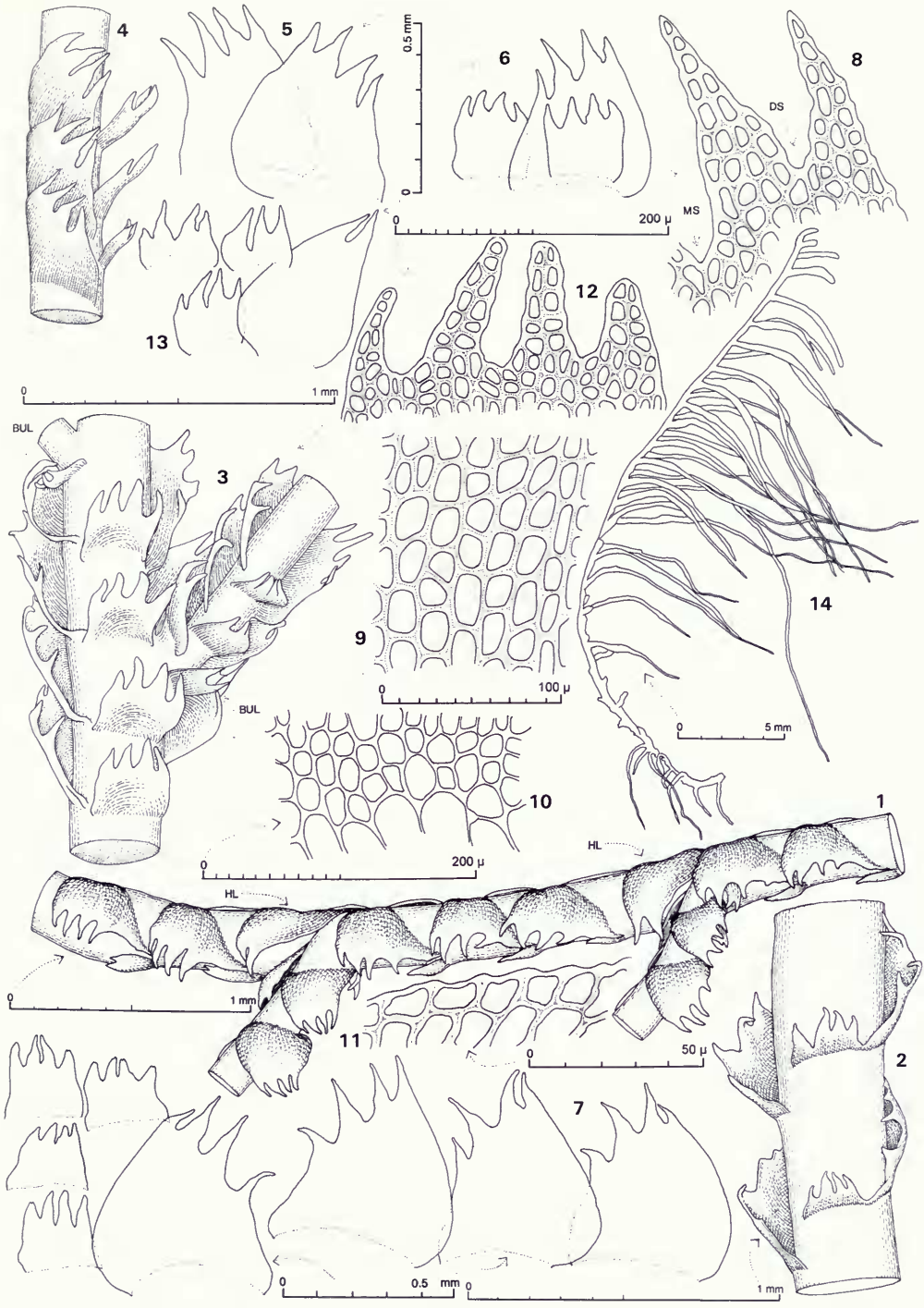

FIG. 13. *Lepidozia procera* Mitt. **1.** Portion of main shoot with 2 *Frullania*-type branches (HL = half-leaf); lateral view. **2.** Portion of main shoot, ventral view. **3.** Sector of main shoot and *Frullania*-type branch, ventral view (BUL = first branch underleaf). **4.** Sector of main shoot, lateral view. **5.** Leaves. **6.** Leaf and within + at left, underleaves. **7.** Four leaves and, at left, underleaves. **8.** Dorsalmost 2 lobes of leaf (ds = dorsal sinus, ms = median sinus). **9.** Median disc cells. **10.** Median-basal cells of leaf showing row of enlarged cells. **11.** Cells of dorsal margin of disc. **12.** Distal sector of underleaf. **13.** Half-leaf (right) and first branch underleaves. **14.** Outline of plant at low magni-

populations, and several leaves should be carefully examined. Cells of the uniseriate row in the leaf lobes are thick-walled, with the septa distinctly thickened and swollen (Fig. 13 : 8).

In ventral aspect the plants are reminscent of *L. microphylla* in having underleaves markedly small for the shoot size; those of *L. procera* are only 0.7–0.9× the diameter of the stem (Fig. 13 : 2, 3). Also, the underleaves often are narrowly connate on one side (Fig. 13 : 2), an unusual feature among New Zealand representatives of the genus, or the underleaves may be free (Fig. 13 : 3).

DISTRIBUTION–ECOLOGY—New Zealand (South Is., North Is.), Tasmania, Australia (Victoria, Queensland). Within New Zealand the species sporadically occurs terricolous or saxicolous in low-elevation (at most 200 m) forests on South Island, and is known from only one station (290 m) on North Island. For example, it occurs on mossy banks in *Nothofagus* forests in Fiordland (*Hatcher 704a*), as well as over rock in a creek bed within a podocarp-dominated forest (Lake Gault, *Engel 21722*). On North Island the species was found on a layer of soil over a huge streambed boulder in a shaded, humid, steep-sided stream valley within a forest mainly of kauri, but with some *Weimannia silvicola* (Waipoua Forest, *Engel 22678*).

SELECTED SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. OTAGO PROV.: Fiordland Natl. Park, head of Lake McKerrow, near McKerrow Hut, *Hatcher 1476* (F); trail between Gunn's Hut and Hidden Falls, ca. 30 miles SE of Lake McKerrow, *Hatcher 704a* (F). WESTLAND PROV.: Jackson Bay, between confluence of Jackson River and Arawata River and Lake Ellery, off Jackson River Road, ca. 30 m, *Child H4253* as *L. microphylla* (F); Westland Natl. Park, track to Lake Gault, NE of Lake Matheson, NW of town of Fox Glacier, ca. 100–200 m, *Engel 21722* (F). NELSON PROV.: Valley of the Little Wanganui River, ca. 0.5 km S of Scobie Clearing, 120 m, *Fife 7116* as *L. laevifolia* (F). NORTH ISLAND. NORTH AUCKLAND PROV.: Waipoua Forest, Waikohatu Stream at Waikohatu Kauri Bridge, 290 m, *Engel 22678* (F).

Lepidozia obtusiloba Steph. Figures 14–16.

Lepidozia obtusiloba Steph., Spec. Hep. 3: 598. 1909. Original material: New Zealand, South Is., *Beckett, Helms.*

Lepidozia parvitexta Steph., Spec. Hep. 3: 598. 1909, *syn. nov.* Lectotype (*nov.*): New Zealand, Jacksons, *Goebel* (G!—c. sporo.).

Plants typically erect, rather flexuous, with laxly spreading (var. *parvula*) to strongly ventrally secund branches that are often parallel to one another, brown to yellow-brown, the shoots small to medium, to 1 cm wide, including branches. Branching nearly exclusively of *Frullania* type, rather short, closely and regularly 1(2)-pinnate, the primary branches sporadically becoming whiplike, flagelliform and microphyllous, the nonmicrophyllous leaves ± symmetrically 4-lobed; secondary branches sporadic, 1(3) per primary branch; branch half-leaf symmetrical, cordate, 2-lobed to ca. 0.2–0.4; first branch underleaf 2–3(4)-lobed, inserted on ventral-lateral side of juncture of main axis and branch and aligned with underleaves of branch or leaves of main shoot. Ventral-intercalary branching occasional, leafy or long stoloniform. Stems rigid. Leaves rigid, brittle, somewhat concave, imbricate and nearly or completely obscuring stem in dorsal view, 0.65–1 mm long at longest point, 0.5–1.2 mm wide at widest point (0.5–0.7 mm wide × 0.7 mm long in var. *parvula*), spreading, the insertion narrow to broad, and weakly incubous; ventral extremity of leaf at times extending up to stem midline, leaves distinctly asymmetrical, unequally 4(5)-lobed, the leaves divided to ca. 0.45–0.65 (median sinus), the distance from dorsal sinus base to insertion much greater than that from ventral sinus to insertion, the dorsal sinus at times reduced to a mere notch. Lobes acute to subapiculate, the 2 dorsal lobes paired, the 2 ventral widely divergent from the united dorsal lobes; dorsal lobes terminating in several laterally juxtaposed cells or a single cell or a uniseriate row of 2–3(4) cells, the cells of uniseriate row ± isodiametric, thick-walled; dorsal lobes entire, 6–8(10) cells wide at base. Disc distinctly asymmetrical, 17–21 cells high at dorsal sinus, 6–10 cells high at ventral sinus, the margins entire, the dorsal margin broadly ampliate, cordate at the base, the ventral much shorter than the dorsal, subcordate. Cells of ventral margin and lobes ± isodiametric, forming border. Cells of disc middle thick-walled, often distinctly so, trigones sometimes present, medium

←

fication, lateral view. (Figs. 1, 2, 7, 11 from *Engel 21722*, New Zealand, South Is., Westland Prov., Westland Natl. Park, track to Lake Gault; remainder from *Hatcher 1476*, New Zealand, South Is., Otago Prov., Fiordland Natl. Park, head of Lake McKerrow.)

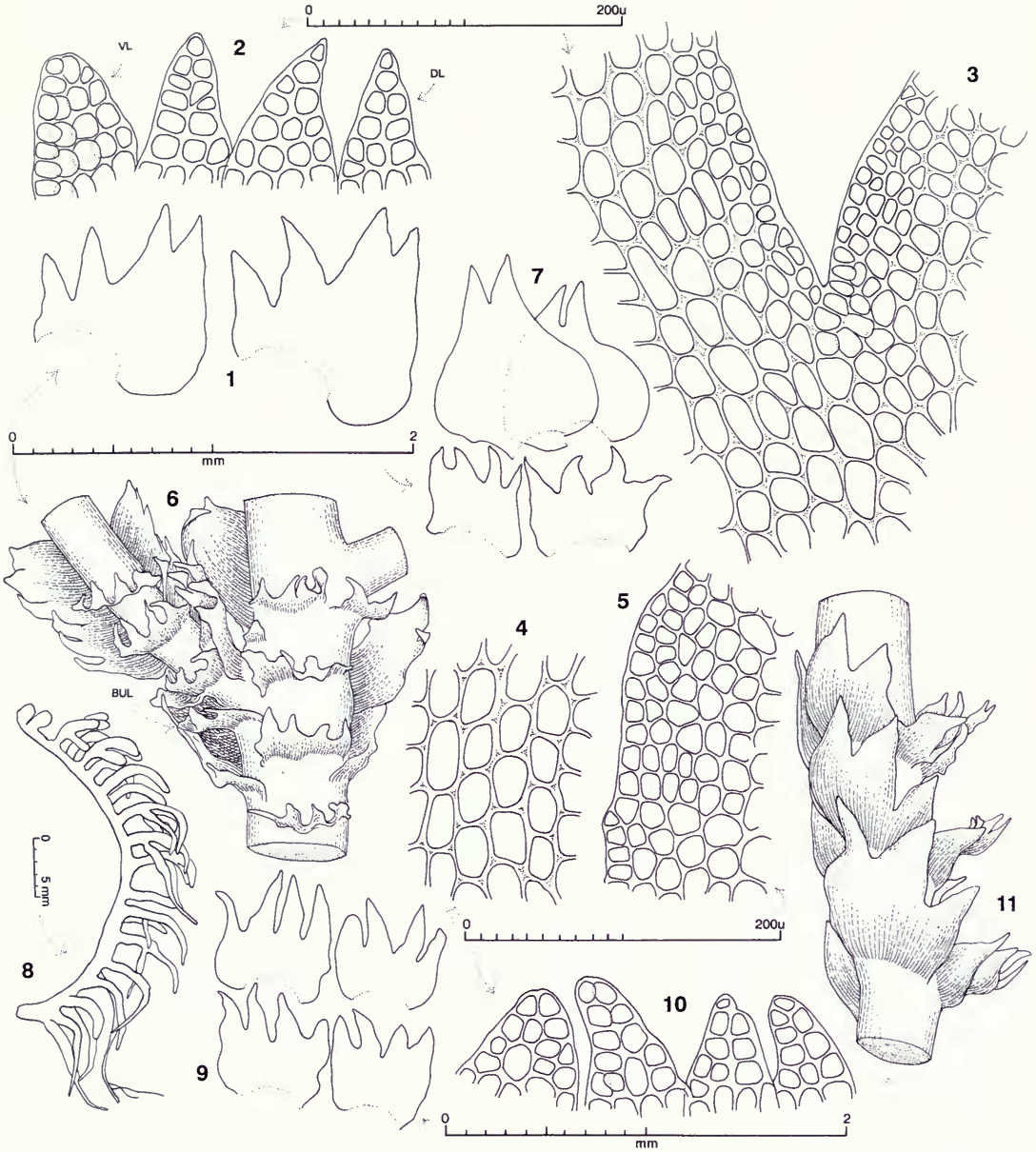

FIG. 14. *Lepidozia obtusiloba* Steph. **1.** Leaves. **2.** Apical sectors of 4 lobes from same leaf (vl = ventral lobe; dl = dorsal lobe). **3.** Base of median sinus of leaf showing border of smaller cells. **4.** Median disc cells. **5.** Sector of ventral margin of leaf disc showing border of smaller cells. **6.** Sector of main shoot with 2 *Frullania*-type branches, ventral view (BUL = first branch underleaf). **7.** Half-leaves and, below, 2 first branch underleaves. **8.** Outline of shoot at low magnification, lateral view. **9.** Underleaves. **10.** Apical sectors of 4 lobes from same underleaf. **11.** Sector of main shoot, lateral view. (All from *Engel 17843,* New Zealand, South Is., Westland Prov., Mt. Aspiring Natl. Park, off track to Mt. Brewster.)

and straight-sided to large and bulging, 19–28 × 24–35(42) μm; median basal cells enlarged, in a single row; cuticle smooth to indistinctly striate to distinctly papillose. Underleaves widely spreading to squarrose, symmetrically 4-fid to ca. 0.4–0.55 (median sinus), the lobes plane to slightly ventrally sulcate, the sinus bases plane to slightly reflexed, the lobes ± parallel to somewhat spread-

ing, short-attenuate, entire, blunt at the tip and terminating in several laterally juxtaposed cells, or with a uniseriate row of 2–3 cells; disc 7–10 cells high at median sinus, the margins parallel, plane, subcordate at base, entire or with a blunt tooth.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, often cernuous ventral-intercalary branches from main shoot; bracts ventricose-cucullate, 2–3-lobed to ca. 0.2–0.3, the lobes acute, often apiculate; disc margins basically entire; antheridia 1–2 per bract, the stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem, the base of gynoecium swollen, bulbous and rhizoidous; bracts of innermost series much larger than leaves, erect and sheathing the perianth, the bracts deeply concave, broadly ovate to suborbicular; apices with 4 abbreviated lobes composed of ± regularly rectangular and subrhomboidal cells, the apical end of the marginal cells only sporadically diverging and forming a tooth, the lobes thus basically smooth and only exceptionally with a crenulation, the lobe summit composed of 2 or more laterally juxtaposed cells, with each lobe terminating in a slime papilla, the lobes at times obsolete, with each represented solely by a slime papilla mounted on 2 laterally juxtaposed cells that project slightly more than neighboring cells; lamina composed of ± regularly subrectangular cells, the margin bordered by thin-walled cells of variable shape and orientation, some hardly longer than wide, others ± rhomboidal, the apical or free end of marginal cells usually only sporadically divergent and forming a crenulation, the margins basically smooth except for sporadic crenulations or a several-celled tooth, or, occasionally, the margin crenulate-denticulate by variously projecting cells; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth, the lobes composed of feebly tiered, often long, narrow, subrectangular to weakly sinuate-rhomboidal, slightly thick-walled cells; mouth cells laterally fused to the summit or nearly so, the mouth thus rather regularly crenulate; perianth cells ± regularly subrectangular below mouth, and here the cuticle is inconspicuously striolate; perianth 2–3 stratose near base.

Seta with 16 rows of outer cells surrounding an inner core of ca. 60 much smaller cells. Capsule long elliptical, the wall 46–48 μm thick, of 4–5 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheetlike thickenings and several large nodules and spines alternating with walls that are devoid of thickenings, the transverse walls usually devoid of thickenings or sporadically have an isolated nodule; innermost layer of cells ± tiered, narrowly rectangular, semiannular bands common, close and numerous, sometimes incomplete, sporadically forked.

Spores 13.5–14.9 μm, exine brown, thin, with dense, sharply defined, close papillae and short vermiculate markings. Elaters rigid, nontortuous, 9.6–10.1 μm wide, slightly tapering toward tips, bispiral, the spirals 3.4 μm wide.

DIFFERENTIATION—The typical form of the species is distinctive because of brownish pigmentation and erect shoots with distinctly ventrally secund branches (Fig. 14 : 8). The species is allied to *L. ornata* but differs in the lack of accessory ornamentation, the broadly acute, united dorsal lobes with a shallow dorsal sinus (in *L. ornata* the lobes are narrowly acute to attenuate and narrowing to a sharp apex), and the essentially plane and unornamented underleaves. Also, the depth of the median sinus tends not to be as great as in *L. ornata,* and the ventral lobes tend to be broader than in that species. The underleaf lobes are often bluntly rounded at the summit (Fig. 14 : 10), giving rise to the name.

Lepidozia obtusiloba has the dorsal leaf bases optimally ampliate (Fig. 14 : 1), and the stem half-leaves tend to have both margins broadly ampliate at the base (Fig. 14 : 7); it has, apparently consistently, a shallow dorsal sinus, descending only 0.2–0.25 the leaf length. Basal branch underleaves are usually 2–3-fid. In leaf form closely approaching *L. laevifolia* var. *alpina.*

Hodgson (in Herzog, 1938) refers *Lepidozia parvitexta* Steph. to *L. breviloba* Steph., a synonym of *L. procera;* however, the lectotype of *L. parvitexta,* labelled "original" by Stephani, is typical *L. obtusiloba,* as is the syntype, leg. Naylor Beckett. Both are abundantly fruiting. Stephani (1909) described the species as "brunneola"; the branches of the type are characteristically ventrally secund, and the underleaves widely spreading and divided to ca. 0.5. Although *L. parvitexta* and *L. obtusiloba* were published simultaneously, the latter is the name in current use for this taxon.

Allison and Child (1975) called attention to the

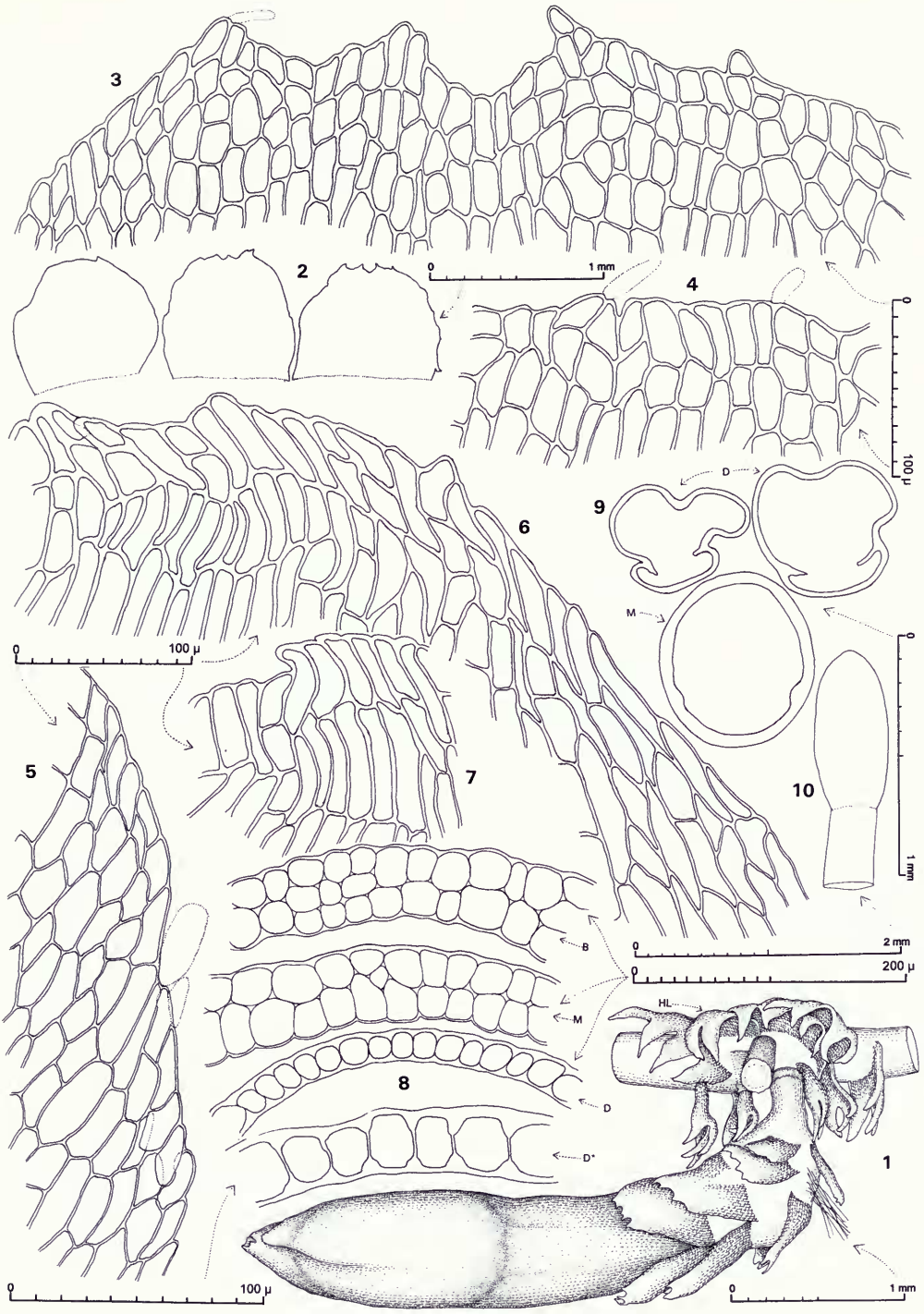

FIG. 15. *Lepidozia obtusiloba* Steph. **1.** Portion of main shoot with mature gynoecium, lateral view. Base of terminal branch shown, but with initial leaves and underleaves removed from branch for clarity (hl = half-leaf). **2.** Innermost bracts and bracteole. **3.** Apex of innermost bract. **4.** Portion of apex of innermost ♀ bract showing obsolete median pair of teeth, each represented by a slime papilla. **5.** Portion of lateral margin of innermost bract showing nearly entire condition. **6.** Perianth mouth, the summit at upper left. **7.** Portion of perianth mouth. **8.** Perianth, cross sections (top to bottom) through basal (= b), median (= m) and distal (= d) sectors; d* drawn at higher magnification.

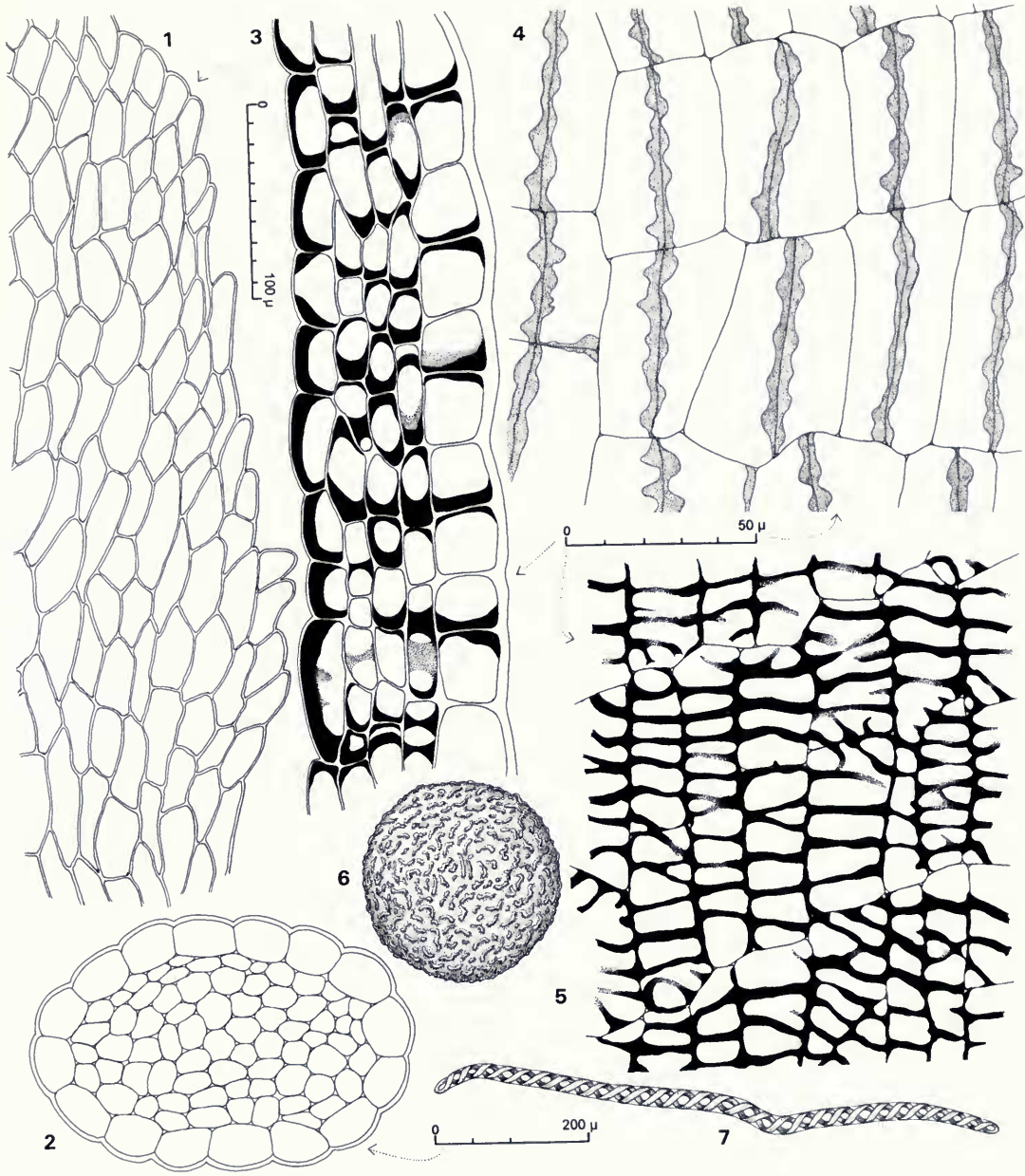

FIG. 16. *Lepidozia obtusiloba* Steph. **1.** Portion of lateral margin of innermost ♀ bract showing crenulate-denticulate condition. **2.** Seta, cross section. **3.** Capsule wall, cross section. **4.** Capsule wall, outer layer. **5.** Capsule wall, inner layer. **6.** Spore (×1880). **7.** Elater (×233). (All from *Engel 17565,* New Zealand, South Is., Otago Prov., S side of Mt. Cargill.)

←

9. Perianth, cross sections through median (= m) and distal portions (= d). **10.** Capsule profile. (All from *Engel 17565,* New Zealand, South Is., Otago Prov., S side of Mt. Cargill.)

presence of 3-lobed branch leaves in this species. We have not been able to verify this character.

The species is separable into two varieties, as follows:

Key to the varieties of *L. obtusiloba*

1. Plants medium (to 1 cm wide, including branches), erect, dark brown; branches strongly ventrally secund; leaves rather broadly inserted, (0.7)0.8–1.2 mm wide × 0.65–1 mm long ..... var. *obtusiloba*
1. Plants small (similar to *L. concinna* in size or smaller), procumbent, brown or yellow-brown to greenish; branches spreading and not distinctly secund; leaves narrowly inserted, easily detached, only 0.5–0.7 mm wide × 0.7 mm long ..... var. *parvula*

Lepidozia obtusiloba Steph. var. ***obtusiloba***

Plants medium (to 1 cm wide, including branches), erect, dark brown; branches strongly ventrally secund; leaves rather broadly inserted, (0.7)0.8–1.2 mm wide × 0.65–1 mm long.

Distribution–Ecology—Auckland Is., New Zealand (South Is.), Australia (Victoria).

A montane variety typically present in the upper reaches of forests of, for example, *Nothofagus menziesii* or *Nothofagus solandri.* It is often abundant, and then appears as the most common hepatic on the forest floor, rotten logs, and tree trunks. Variety *obtusiloba* may extend to the subalpine and alpine zones in protected niches on the faces of boulders or cliffs.

Selected Specimens Seen—AUCKLAND IS.: E end of Hooker Hills, 396 m, *Johnson 7/32* (WELT). NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Takahe Valley, W of W side of Lake Te Anau, *Mark* (F); Fiordland Natl. Park, Gertrude Valley, off track to Gertrude Saddle, NE of Homer Tunnel, 1880–1900 m, *Engel 18864* (F); ibid., S end of Lake Marion, W of Hollyford River, 695 m, *Engel 23183* (F). SOUTHLAND/OTAGO PROV. BOUNDARY: Key Summit, NNE of Lake Gunn, ca. 915 m, *Child H2585* (F). OTAGO PROV.: Ajax Swamp, ca. 1 km N of Ajax Hill, Catlins River area, ca. 610 m, *Child H5523* (F); Maungatua, W of Mosgiel, ca. 825 m, *Child 139* (F); S side of Mt. Cargill, just below summit, N of Dunedin, ca. 670 m, *Engel 17565*—c. sporo. (F); unnamed peak immediately NE of Mt. Cargill, N of Dunedin, ca. 550 m, *Engel 17585* (F); Blue Mts., 915 m, *Child 389* (F); Fiordland Natl. Park, trail between Gunn's Hut and Hidden Falls, ca. 30 mi SE of Lake McKerrow, *Hatcher 607* (F); ibid., head of Lake McKerrow, *Hatcher 725* (F); Paradise, Dart Valley, N of N end of Lake Wakatipu, ca. 610 m, *Child H107* (F); Mt. Aspiring Natl. Park, Blue Valley Track, above Blue River just N of confluence with Makaroa River, 430–480 m, *Engel 21916* (F); ibid., ridge below and W of Mt. Shrimpton, 1250 m, *Engel 17856*—c. sporo. (F); tributary of Siberia Stream, opposite Siberia Hut, WNW of Makarora, ca. 760 m, *Child H2990* (F). OTAGO/WESTLAND PROV. BOUNDARY: Haast Pass, ca. 610 m, *Child H4504*—c. ♂ + per. (F). WESTLAND PROV.: Mt. Aspiring Natl. Park, off track to Mt. Brewster, below and W of Mt. Armstrong, SW of Mt. Brewster, ca. 900 m, *Engel 17843*—c. per. (F); Westland Natl. Park, Franz Josef Glacier Valley, Roberts Point, SW of Mt. Gunn, ca. 620–670 m, *Engel 18113*—c. per. (F); upper Otira Valley, ca. 1220 m, *Child H5266* (F); Camp Creek, W of Alexander Range, 1040 m, *Reif C259F*—c. sporo. (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass, *Beckett 725,* syntype of *L. parvitexta* (G—c. sporo.); Arthur's Pass Natl. Park, Arthur's Pass, near Temple Basin Ski area, *Engel 6456* (F); ibid., Bealey Valley Track, ca. 875–900 m, *Engel 22865* (F). CANTERBURY PROV.: Cass, Woolshed Hill, *Visch s. n.* (F); Arthur's Pass Natl. Park, Scotts Track to Avalanche Peak, W of town of Arthur's Pass, 950 m, *Engel 22083* (F); ibid., immediately below Punchbowl Falls, *Engel 6874A* (F); Bealey Spur, within 3 km W of beginning of track to Bealey Spur Hut, ca. 825 m, *Fife 6717* (F); Arthur's Pass Natl. Park, Bealey River, off Bealey Valley Track, 830–850 m., *Engel 18508* (F); Spencer Mts., opposite Ada Hut, ca. 915 m, *Child 4611* (F). NELSON/CANTERBURY PROV. BOUNDARY: Spencer Range, Mt. Gloriana, ca. 1675 m, *Child H3965A* (F). NELSON PROV.: Nelson Lakes Natl. Park, Pinchgut Track, W of southern sector of Lake Rotoiti, SSW of St. Arnaud, ca. 1280–1390 m, *Engel 21401*—c. per. (F); St. Arnaud Range, Rainbow Skifield just below ski-tow area, E of S end of Lake Rotoiti, 1210 m, *Engel 22805* (F); Flora Hut, NW Nelson S. F. Park, ca. 915 m, *Child H4770* (F); Abel Tasman Natl. Park, Mt. Evans, ca. 1065 m, *Child H4703A* (F). MARLBOROUGH NEAR BOUNDRY WITH NELSON PROV.: Mt. Richmond Forest Park, Red Hills, track to Maitland Hut, NE of St. Arnaud, ca. 700–920 m, *Engel 21445* (F). MARLBOROUGH PROV.: Richmond Range, Mt. Richmond, ca. 1220 m, *Child H4335* (F); Mt. Fishtail, ca. 1220 m, *Child H3240* (F); Mt. Robertson, SES of Picton, ca. 1035 m, *Child H4392* (F).

Lepidozia obtusiloba var. ***parvula*** Engel, var. nov.

Plantae parvae, amplitudini L. concinnae similes vel minores plerumque procumbentes brunneae flavobrunneae vel virescentes; rami patentes subsecundi.

Holotype—New Zealand, South Is., Westland Prov., Arthur's Pass Natl. Park, Kelly Range, vicinity of Carroll Hut, above Kellys Creek, N of Otira, 1150 m, *Engel 18382* (F); isotype: (CHR).

Plants small (similar to *L. concinna* in size or smaller), procumbent to (exceptionally) suberect, brown to yellow-brown to greenish; branches

spreading and not distinctly secund; leaves narrowly inserted, easily detached, 0.5–0.7 mm wide × 0.7 mm long.

DIFFERENTIATION—A small extreme of the species, *L. obtusiloba* var. *parvula* typically occurs in rock crevices or on dripping rock faces in alpine situations, but it is also encountered, although sporadically, at median or lower elevations. Plants assigned to the variety have an appearance quite distinct from that of the more typical, well-developed plants of the species, being typically procumbent, with branches spreading and not distinctly secund. The leaves are smaller than in var. *obtusiloba*, more narrowly inserted and easily detached, and have disc cells often more strongly thick-walled. The color varies from brown to pale yellowish brown to greenish. They share with the typical form a brownish pigmentation, similarly shaped (though smaller) leaves, and shallowly lobed, widely spreading to squarrose underleaves.

The variety may be distinguished from *L. concinna* by the presence of brown pigments or (when greenish) by the shorter, broader underleaf lobes, the distinctly asymmetrical leaves with a shallow dorsal sinus (which may be reduced to a mere notch), and the smaller, thick-walled median disc cells. It differs from *L. laevifolia* by the larger shoot size, the presence of brown pigments, and the imbricate, strongly asymmetrical leaves that are not distinctly cup-shaped when dry.

DISTRIBUTION–ECOLOGY—New Zealand (South Is., North Is.). *Lepidozia obtusiloba* var. *parvula* typically occurs in rock crevices or on damp to dripping, often shaded, rock faces in alpine or subalpine sites (in the latter case, particularly under shrub cover, and here sporadically terrestrial). It also may occur in very wet niches, such as at the edges of tarns between tussock and covered by a layer of old tussock blades (Mt. Robert Skifield, *Engel 22834*). On vertical banks of alpine rills, it may form very tight, compact populations with little more than the tips of each shoot exposed (Old Man Range, *Engel 23256*). The variety also (sporadically) occurs in upper-elevation forests of *Nothofagus menziesii* or *N. solandri* var. *cliffortioides* and only rarely at median or lower elevations (examples: on old logs at 460 m in the Mt. Cargill area and at 135 m in the Cascade ultramafic moraine area in southern Westland). At the Cascade Road site var. *parvula* occurs on the floor in an area consisting of ultramafic rocks and outcrops with rather open vegetation consisting mainly of *Gleichenia, Lycopodium, Juncus,* the lichen *Cladina,* and scattered *Leptospermum.*

SELECTED SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. OTAGO PROV.: Ajax Swamp, ca. 1 km N of Ajax Hill, Catlins River area, ca. 550 m, *Child H5546* (F); Maungatua, W of Mosgiel, ca. 760 m, *Child 2843* (F); Mt. Cargill, N of Dunedin, ca. 455–700 m, *Child 962, 2685* as *L. ?concinna* (F); Kakanui Range, ca. 1525 m, *Child H2836* (F); Rock & Pillar, ca. 1315 m, *Child 488* (F); Old Man Range, Symes Road, 1370–1570 m, *Engel 23256* (F); Jordan River, head of Lake Wakatipu, vicinity of Paradise, ca. 455 m, *Child H1218* as *L. laevifolia* (F); Mt. Aspiring Natl. Park, below and W of Mt. Shrimpton, ca. 1220 m, *Child H4803* (F). WESTLAND PROV.: Cascade Road, Cascade ultramafic moraine, W of Martyr Saddle, SSW of Jackson Bay, 135 m, *Engel 23002*; Mt. Aspiring Natl. Park, Cross Creek, 1.1 km N of Haast Pass, 540 m, *Engel 21879* (F); Mt. Brewster, ca. 1435 m, *Schuster 67-459a* (F); upper Otira Valley, ca. 1220 m, *Child H5257* (F); Arthur's Pass Natl. Park, Kelly Range, vicinity of Carroll Hut, above Kellys Creek, N of Otira, 1150 m, *Engel 18382* (F); ibid., Otira River gorge, W of Arthur's Pass, ca. 305–365 m, *Schuster 48493* (F); Arthur's Pass, Otira side, 760 m, *Child 336* (F); Camp Creek, W of Alexander Range, 800–1040 m, *Reif C150B, C259J* (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Arthur's Pass, near Temple Basin Ski area, *Engel 6454C* (F); ibid., Otira Valley Track, along Otira River, NE of Mt. Rolleston, 1210–1310 m, *Engel 22896* (F). CANTERBURY PROV.: Mt. Cook Natl. Park, Sealy Range, below Sealy Lakes, ca. 1280 m, *Schuster 49711* (F); near summit of Mt. Tourlesse, *Hatcher 1216* (F); Arthur's Pass, ca. 915 m, *Child H 2078* (F). NELSON/CANTERBURY PROV. BOUNDARY: Spencer Range, Mt. Gloriana, ca. 1525–1830 m, *Child H3967, H3983* (F). NELSON PROV.: Nelson Lakes Natl. Park, E slope of Robert Ridge in vicinity of Mt. Robert Skifield, W end of Lake Rotoiti, 1400–1480 m, *Engel 22834* (F); St. Arnaud Range, Rainbow Skifield, E of S end of Lake Rotoiti, 1360–1480 m, *Engel 22759* (F). MARLBOROUGH PROV.: Richmond Range, Mt. Richmond, ca. 1615 m, *Child H4316* (F); Mt. Fishtail, ca. 1370 m, *Child H4340* (F). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, Soda Springs, Mangatepopo Stream, 1350 m, *Engel 22481* (F); ibid., Taranaki Falls Track, E of Whakapapa Village, 1240 m, *Engel 22469* (F). GISBORNE/SOUTH AUCKLAND PROV. BOUNDARY: Urewera Natl. Park, track to Whakataka Hut from Lake Waikaremoana, N of western extremity of Lake Waikaremoana, 1000–1100 m, *Engel 23308* (F). GISBORNE PROV.: Urewera Natl. Park, Huiarau Range, summit area of Te Rangaakapua, 1265–1320 m, *Engel 23378* (F).

***Lepidozia ornata* Engel, sp. nov.** Figure 17.

Plantae brunneae; rami patentes; folia amphigastriaque et lobis accessoriis et additamentis paraphyllaceis et lamellis varie ornata.

HOLOTYPE—New Zealand, South Is., Westland

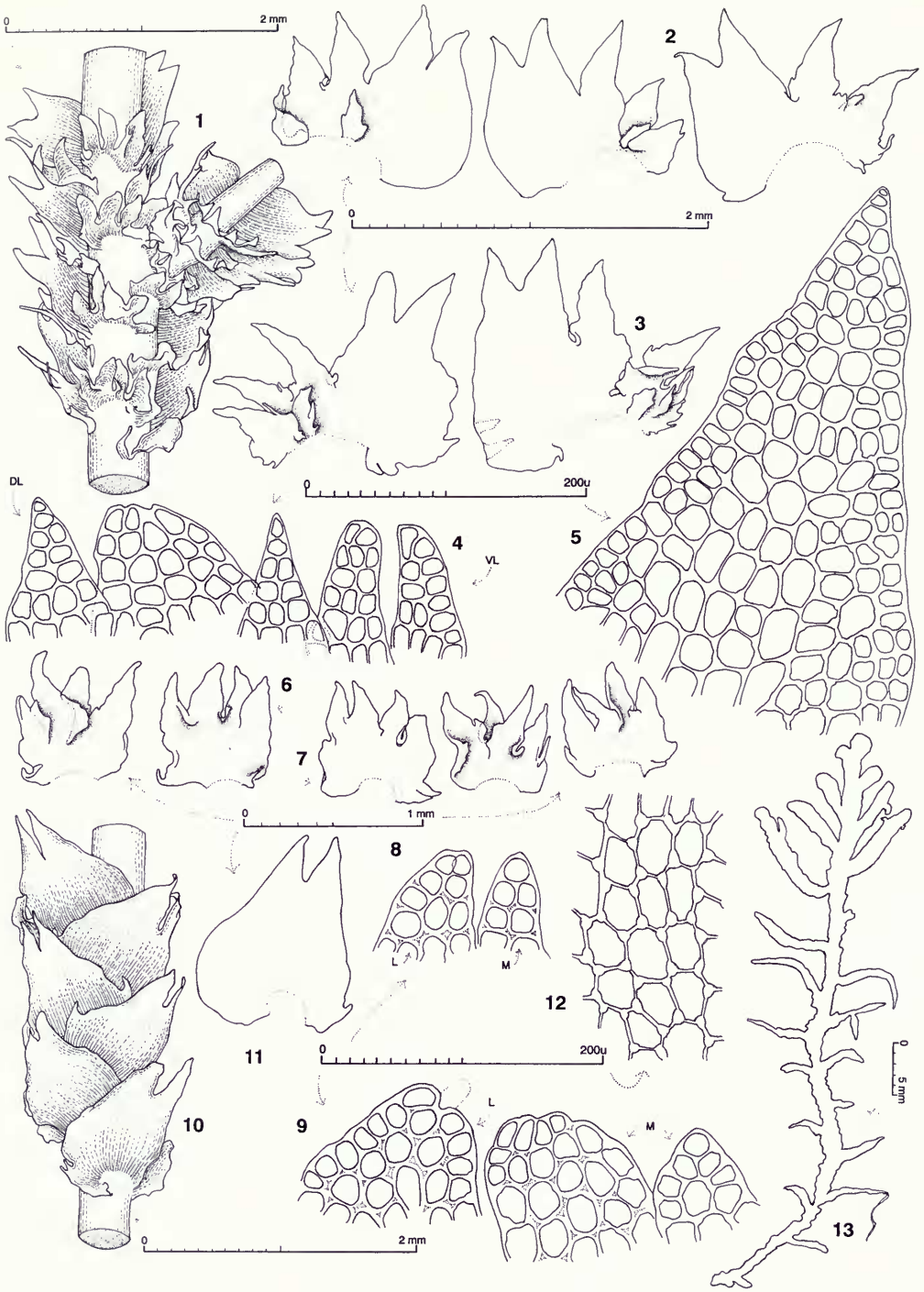

FIG. 17. *Lepidozia ornata* Engel. **1.** Sector of main shoot with *Frullania*-type branch, ventral view. **2, 3.** Leaves. **4.** Apical sectors of 5 lobes from same leaf (dl = dorsal lobe; vl = ventral lobe). **5.** Second dorsalmost leaf lobe. **6, 7.** Underleaves. **8.** Apical sectors of lateral (L) and median (M) lobes of same underleaf. **9.** Apical sectors of median (M) and lateral (L) lobes of same underleaf. **10.** Sector of main shoot, dorsal view. **11.** Half-leaf. **12.** Median disc cells of leaf. **13.** Outline of shoot at low magnification. (Figs. 1, 3–7, 10, 12, 13 from type; 2, 8, 9, 11 from *Engel 18799,* New Zealand, South Is., Fiordland Natl. Park, Mistake Creek.)

Prov., Mt. Aspiring Natl. Park, below and W of Mt. Armstrong, SSW of Mt. Brewster, ca. 1250–1450 m, *Engel 17789* (F); isotype: (CHR).

Plants suberect, stiff and wiry, rather flexuous, with spreading to weakly ventrally secund branches, warm brownish, the shoots medium, to 2.4 cm wide, including branches. Branching nearly exclusively of *Frullania* type, rather short, the pattern variable: distantly and irregularly to regularly 1(2)-pinnate, the primary branches sometimes becoming whiplike, flagelliform, and microphyllous, the nonmicrophyllous leaves asymmetrically to subsymmetrically 4-lobed, the primary branches sometimes developing into new leading shoots; secondary branches occasional, 1–2 per primary branch; branch half-leaf subsymmetrical, cordate, 2-lobed to ca. 0.3, the base variously armed with teeth and accessory appendages; first branch underleaf 2–4-lobed, inserted on main axis or ventral-lateral side of juncture of main axis and branch and aligned with underleaves of branch. Ventral-intercalary branching not seen. Stems somewhat flexuous. Leaves rigid, brittle, concave, imbricate and completely obscuring stem in dorsal view or nearly so, 0.9–1.2 mm long at longest point, 1–1.6 mm wide at widest point, spreading, the insertion weakly to moderately incubous, recurved at dorsal end; ventral extremity of leaf at times extending to stem midline, the ventral lobe often aligned with lateral underleaf lobes, ± decurrent on the stem or the lobe with a decurrent lobuliform flap. Leaves distinctly asymmetrical, unequally 4(5)-lobed and variously appendaged, the leaves divided to ca. 0.5–0.85 (median sinus), the distance from dorsal sinus base to insertion much greater than that from the median and ventral sinuses to insertion. Lobes narrowly acute to attenuate to acuminate, the dorsal pair of lobes paired, the 2 ventral widely divergent from the united dorsal lobes (when flattened), the ventral 1 or 2 lobes often ventrally sulcate, subfalcate, sometimes with a tooth, the lobes terminating in several laterally juxtaposed cells, or a single cell or a uniseriate row of 2–3 cells, the cells of uniseriate row ± isodiametric, thick-walled; dorsal lobes entire, usually narrowing to a sharp apex, 8–14 cells wide at base; ventral and median sinuses reflexed, with accessory armature often present in the sinus base. Disc distinctly asymmetrical, 20–25(31) cells high at dorsal sinus, 8–10 cells high at ventral sinus, the dorsal margin broadly ampliate, often distinctly auriculate at the base, sporadically with a tooth or spine near the base, the ventral margin much shorter than the dorsal, subcordate to subauriculate, typically with accessory armature. Accessory lamellae sometimes present on the abaxial face of disc, descending from sinus bases. Flattened paraphyllia-like, irregularly dentate appendages often present on base of disc. Marginal cells of disc and lobes ± isodiametric, forming an indistinct border. Cells of disc middle with moderately thickened walls, with intermediate thickenings and medium and straight-sided to large and bulging trigones, 19–27 × 28–40 μm; median basal cells larger, in a single, sometimes indistinct row; cuticle smooth to finely striate-papillose. Underleaves plicate, widely spreading, symmetrically 4-fid to ca. 0.5–0.6 (median sinus), the lobes typically ventrally sulcate, with strongly reflexed sinus bases, accessory lamellae, and flattened paraphyllia similar to those of the leaves; the lobes ± parallel to slightly diverging, short attenuate, the margins entire to irregularly crenulate, often bluntly rounded at the tip or terminating in a uniseriate row of 2(3) cells; disc 8–10 cells high at median sinus, the margins reflexed, subauriculate at base, decurrent, often toothed, rarely with underleaf margin confluent with the ventral leaf margin, or adnate to face of leaf disc.

Plants dioecious. Androecia determinate, on tightly spicate, often cernuous ventral-intercalary branches from main shoot and primary branches (in leafy sectors); bracts ventricose-cucullate, 2-lobed to ca. 0.3, the lobes broad acute, at times apiculate; dorsal margin of disc dilated and broadly and evenly rounded, the dilated portion with several slime papillae and sometimes a tooth, the disc otherwise entire; antheridia 1 per bract, the stalk biseriate. Gynoecia unknown.

DIFFERENTIATION—The combination of brown plants with ornamented leaves and underleaves will immediately distinguish this plant. Leaves and underleaves are variously appendaged with accessory lobes, paraphyllia-like appendages, and lamellae (Fig. 17 : 1–3, 6, 7, 10). The decurrent ventral extremity of the leaf often extends to the ventral stem midline, and at times is ornamented with accessory lobes (Fig. 17 : 1). The ventral and median sinus bases of leaves and sinus bases of underleaves are frequently broadly dilated and the reflexed margins of the lobes often extend downward as irregular lamellae on the abaxial face of the disc. The flattened paraphyllia-like appendages, often at the base of the disc, are present in no other New Zealand species of *Lepidozia* and

are reminiscent of the disc armature of *Pachyschistochila berggrenii* Engel & Schust., also of New Zealand.

See comments under *L. obtusiloba* regarding similarities.

DISTRIBUTION–ECOLOGY—New Zealand (South Is., North Is.). This species is nearly always subalpine to alpine and occurs under snow tussock (*Chionochloa*) cover (often on damp ground between tussock bases), particularly on damp slopes or streambanks (?perhaps requiring adequate drainage). Also present over leaf litter at the edges of tarns, in crevices of cliff faces, and in pockets of banks. The sole record of the species in South Island forests is from the upper reaches of an open *Nothofagus menziesii* forest at 610 m at Moraine Creek, where it forms thick, deep masses on the sides of bryophyte mounds.

SELECTED SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Fiordland Natl. Park, below Mt. Burns, E of Borland Saddle, S of South Branch of Borland Burn, W of Monowai, 1225–1320 m, *Engel 18614* (F); ibid., Mt. Burns, ca. 1370–1525 m, *Child H5094, 5206* (F); ibid., Gertrude Valley, near track entrance to Gertrude Saddle, E of Homer Tunnel, 1740 m, *Engel 21948* (F); ibid., Central Earl Mts., Mistake Creek, between Triangle Peak and Melita Peak, NE of N end of Lake Te Anau, 740–800 m, *Engel 18799* (F); ibid., Moraine Creek Track, area N of Moraine Creek, W of Hollyford River, 610 m, *Engel 23212* (F). OTAGO PROV.: Blue Mts., Tapanui, 915 m *Child 382* (F). WESTLAND PROV.: Mt. Aspiring Natl. Park, below and W of Mt. Shrimpton, 1370–1470 m, *Engel 17863* (F); Westland Natl. Park, track to Alex Knob, off track to Louisa Peak, 1170 m, *Engel 18974*—c. ♂ (F); upper Otira Valley, ca. 1220 m, *Child H5258*—c. ♂ (F); Arthur's Pass Natl. Park, Kelly Range, off track to Carroll Hut, above Kellys Creek, N of Otira, 1040–1110 m, *Engel 18407* (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Otira Valley Track, along Otira River, NE of Mt. Rolleston, 1060 m, *Engel 22915* (F). CANTERBURY PROV.: Mt. Cook Natl. Park, Stocking Stream, SW facing cliffs above Hooker Valley, 1280–1330 m, *Engel 18249* (F). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, Mangatepopo Stream below Soda Springs, ENE of National Park, ca. 1200 m, *Engel 21373* (F).

Lepidozia concinna Col. Figures 6 : 4–7; 18, 19.

Lepidozia concinna Col., Trans. & Proc. New Zealand Inst. 18: 244. 1886. Original material: New Zealand, Waipawa Co., near Norsewood, 1885, *Colenso a. 1417* (BM!, WELT!).

Lepidozia latiloba Col., Trans. & Proc. New Zealand Inst. 19: 287. 1887 (1886). Original material: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso a. 1421* (BM!, WELT!).

Lepidozia colensoana Steph., Spec. Hep. 3: 597. 1909, *syn. nov.* Original material: New Zealand, Lake Waikare, *Colenso 1021* (G!—c. per. + seta).

Plants procumbent, the stems interwoven, rather flexuous, with spreading branches, green, highly nitid, the shoots medium, to 1.7 cm wide, including branches. Branching nearly exclusively of *Frullania* type, often long, closely and regularly pinnate, the primary branches often becoming whiplike, flagelliform, microphyllous and rooting in the substrate, the nonmicrophyllous leaves ± symmetrically 4-lobed; primary branches often developing into new leading shoots; secondary branches occasional, 1–3 per primary branch; branch half-leaf symmetrical, cordate, 2-lobed to ca. 0.3; first branch underleaf 2–4-lobed, inserted on ventral to ventral-lateral side of branch and aligned with underleaves of branch. Ventral-intercalary branching occasional, leafy. Stems flexuous. Leaves when dry curved ventrally, the shoots (particularly branches) then appearing braided, the main shoot leaves concave, loosely imbricate and not obscuring stem in dorsal view, 0.6–0.85 mm long at longest point, (0.7)0.8–1 mm wide at widest point, spreading, the insertion weakly to strongly incubous; leaves variable in shape on the same stem, subsymmetrical to weakly asymmetrical (except for the ampliate dorsal base), subequally 4(5)-lobed, the leaves divided to ca. 0.4–0.6 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion, the dorsal sinus shallow or the sinuses gradually becoming deeper ventrally; dorsal sinus U-shaped, at least at base. Lobes acute to apiculate, not noticeably in pairs (except on asymmetrical leaves), entire, terminating in a uniseriate row of 2–3(6) cells, the cells of uniseriate row ± isodiametric, thick-walled; dorsal lobes 5–7(9) cells wide at base; cuticle of lobes smooth or finely striate-papillose. Disc subsymmetrical, 12–19 cells high at dorsal sinus, 9–11 cells high at ventral sinus, the margins entire, the dorsal margin ampliate but not strongly so, ± cordate at the base, the ventral not much shorter than the dorsal. Cells in a well-defined, large median field, ± isodiametric to occasionally oblong-hexagonal, thick-walled, trigones medium and straight-sided to large and bulging (rarely weak and concave-sided), (24)26–41 μm wide × (32)34–45(49) μm long; cells of the ampliate portion smaller; median basal cells not sharply differentiated; cuticle of disc smooth. Oil-bodies in median subapical cells (1)2–5(6) per cell, coarsely botryoidal, small, spherical to ovoid, 3.6–4 × 3.6–5 μm up to 5 ×

11 μm; basal cells with 4–8 oil-bodies of similar size (4 × 5 μm to 4.5–5 × 6–9 μm). Underleaves inserted on 10 rows of stem cells, widely spreading, ca. 1–1.2× stem width, narrowed to insertion, symmetrically 4-fid to ca. 0.45–0.55 (median sinus), the lobes incurved, plane, somewhat spreading, slenderly attenuate, entire, terminating in a single cell or uniseriate row of 2–3(5) cells; disc 7–9 cells high at median sinus, the margins plane, broadly curved, entire.

Androecia not seen. Perianth (*fide* Stephani, 1909) broadly oblong, 4–6 cells thick at base, the mouth constricted and entire; capsule broadly oval; spores 18 μm, reddish brown; elaters bispiral, laxly twisted.

DIFFERENTIATION—The leaves of *Lepidozia concinna* are variable in shape on the same shoot but typically are subsymmetrically to weakly asymmetrically lobed, with the lobes not notably (and never consistently) in pairs (Fig. 18 : 3, 4). The underleaves are somewhat wider than the stem, narrowed to the insertion (Fig. 18 : 1, 2), inserted on 10 rows of stem cells (Fig. 18 : 11), and with the lobes slenderly attenuate and often broadly incurved (Figs. 18 : 1, 2; 19 : 1). The plants are uniformly green, lacking secondary pigmentation, which will immediately distinguish this species from the *L. obtusiloba* complex. A notable feature of this species is the well-defined median field of large disc cells (to 40 μm wide); the cells are in large part ± isodiametric and typically have medium to large and bulging trigones (Fig. 18 : 6, 7). A few basal cells may be quite large, 25–35(42) × 35–48(56) μm versus 22 × 25–32(36) μm in the lobes (compare Fig. 6 : 5, 6). *Lepidozia concinna* is usually readily recognized because of the deeply lobed underleaves, with attenuated lobes, often 3–4 cells broad at the base (Figs. 18 : 8, 11; 19 : 5, 6).

Mature sporophytes of *L. colensoana* are described by Stephani (1909). The type of *L. colensoana* bears a perianth with an exerted seta, but no capsules were seen; the material is too scanty to bear examination of fertile structures. This is the only fruiting material of *L. concinna* known.

This species is rather similar in leaf form to *L. pendulina* (compare Fig. 10 : 3, 4) but has much smaller appendages; leaves average ca. 615–700 μm broad × 555–620 μm long versus 1640 μm broad × 1300 μm long for *L. pendulina*. The underleaves of *L. pendulina* differ from those of *L. concinna* in being (often) weakly to distinctly plicate, with lamina margins less curved and much less narrowed toward the base (cf. Fig. 10 : 1) and with lobes ventrally sulcate.

In *L. concinna* median cells are ca. 26–41× 34–45 μm; they each have (1)2–5(6) oil-bodies each, small and coarsely botryoidal, ranging from 3–4 μm to 4 × 5 to 3 × 6 up to 5–5.5 × 10–11 μm. Basal cells are ca. 25–35 × 33–46 μm and have 4–8 oil-bodies each; they are similar to those of median cells and are scarcely larger (4 × 4–7 to 4.5 × 6 to 5 × 9 μm), similarly botryoidal.

Plants of *Schuster 67-237a* (Fig. 6 : 4–7) have rather similar leaves, as regards outline and lobing, as does *L. pendulina* (Fig. 10 : 3); both have dorsal leaf bases ampliate, but not strongly so; both have the two dorsal lobes both set off as a unit from the ventral lobes. Both have a narrow, very sharp ventral lobes. There are clear differences in oil-body numbers. In *L. concinna* cells of the leaf middle and distal sectors have (1)2–5(6) oil-bodies each (Fig. 6 : 5) and the basal cells have mostly 4–8 oil-bodies each (Fig 6 : 6). In *L. pendulina* the upper laminar cells have (2)3–8(14) oil-bodies (Fig 6 : 1), and the basal cells bear mostly 16–20 oil-bodies each (Fig. 6 : 2). Basal cells in *L. concinna* are mostly 26–35 × 33–48 μm (Fig. 6 : 6); in *L. pendulina* at least a small area has basal cells to 40–43 × 55–60 μm (Fig. 6 : 2).

For additional comments, see under *L. pendulina* and *L. obtusiloba* var. *parvula*.

NOTES—The type collection of *L. concinna* consists of rather weak, lax, suboptimal shoots with leaves moderately asymmetrical. However, some sectors of shoots have leaves more typical of the species, and show weakly asymmetrical leaves with the distinct field of large median disc cells characteristic of this species.

DISTRIBUTION–ECOLOGY—New Zealand (South Is., North Is.), Tasmania. A forest plant, often in extensive patches and becoming abundant, occurring on old, rotten logs or, less often, over soil; the species occurs along a broad elevational gradient (150–920 m).

SELECTED SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. SOUTHLAND: Lake Hauroko, ca. 215 m, *Child H1542* (F); Waikaia, Heriot Rd, ca. 610 m, *Child H3920* (F); N of Te Anau, *Hatcher 1515* (F); immediately N of Ten Mile Bush, near W shore of Lake Te Anau and ca. 20 km N of town of Te Anau, 200 m, *Engel 23201* (F); around Smithy Creek on road from Te Anau to Milford Sound, ca. 15 km S of Lake Fergus, *Raven 26644A* (F). OTAGO PROV.: Blue Mts.. Black Gully, near Tapanui, 610 m *Child 20* (F); Mt. Cargill, N of Dunedin, ca. 455 m, *Child 2308* (F); Morrisons Creek, N of Dunedin, ca. 305 m, *Child 1318* (F); Jordan

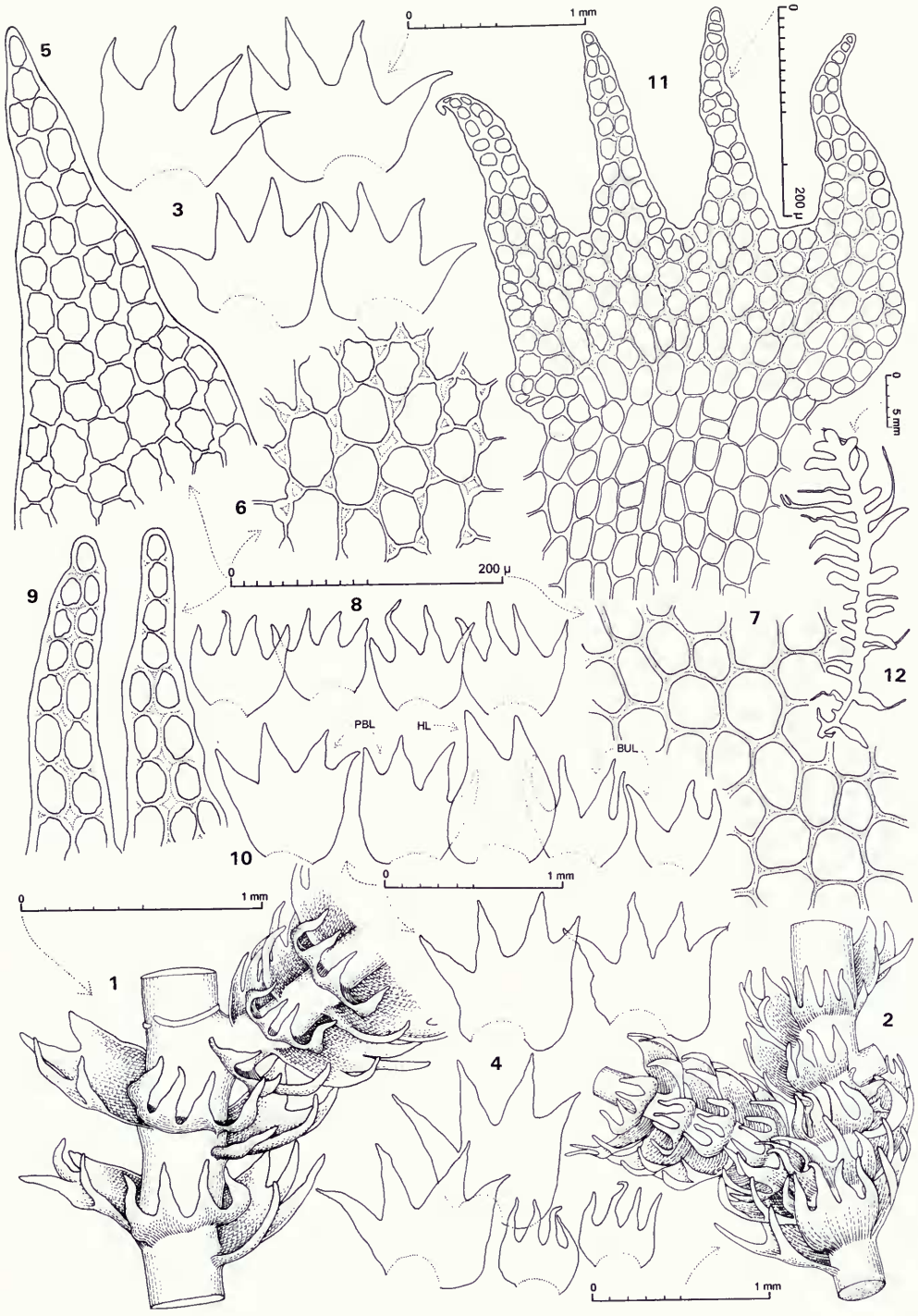

FIG. 18. *Lepidozia concinna* Col. **1.** Portion of main shoot with *Frullania*-type branch, ventral view. Note position of first branch underleaf. **2.** Portion of main shoot with two *Frullania*-type branches, ventral view. **3.** Leaves. **4.** Four leaves and (lower right) 2 underleaves at same scale. **5.** Dorsal lobe of leaf. **6, 7.** Median disc cells of leaf. **8.** Underleaves (drawn at same scale as Fig. 4). **9.** Apical sectors of 2 median lobes of same underleaf. **10.** Primary branch leaves (PBL), half-leaf (HL), and first branch underleaves (BUL). **11.** Portion of stem with underleaf. Note

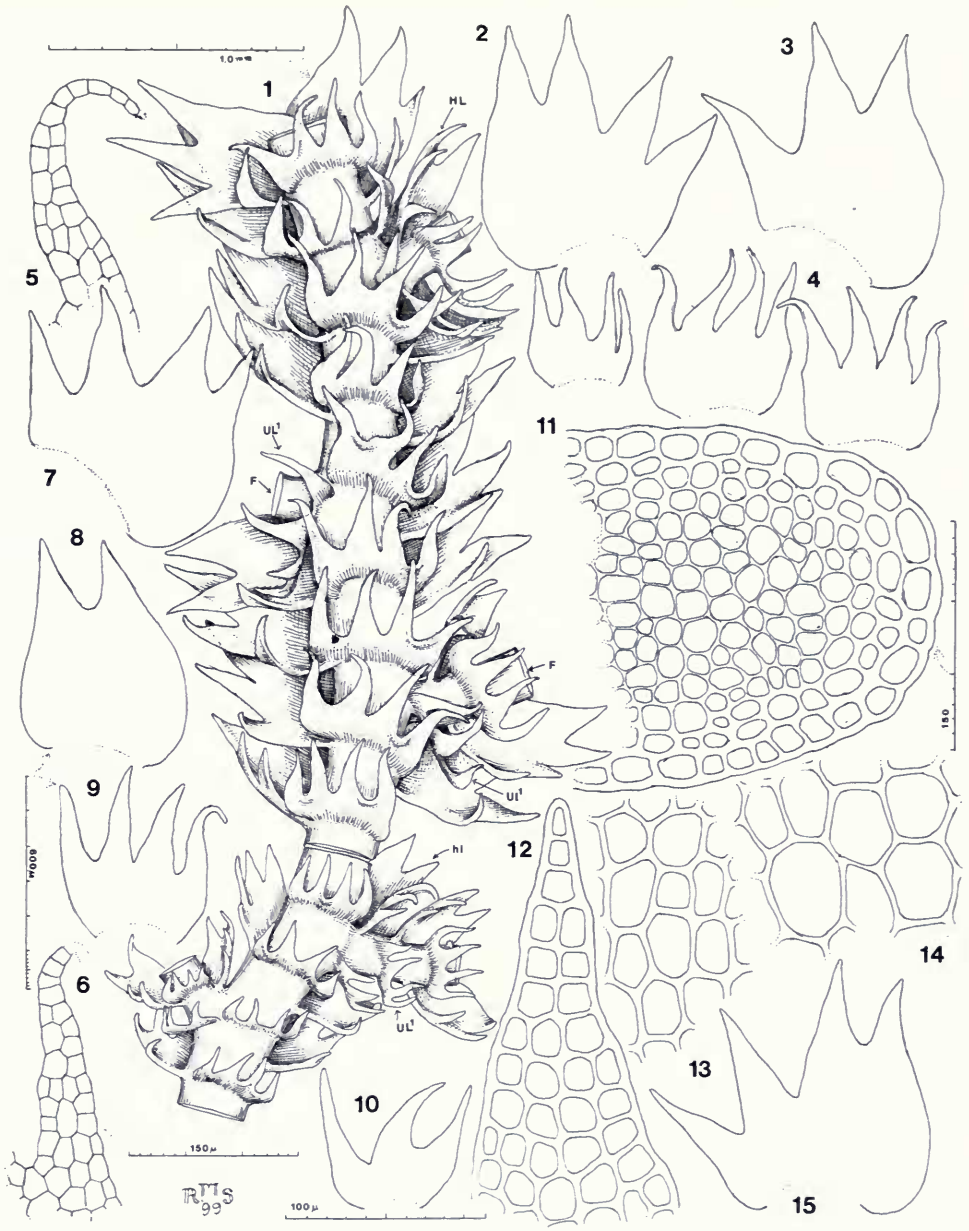

FIG. 19. *Lepidozia concinna* Col. **1.** Part of main stem, ventral aspect, with a sector (below) omitted. Note five *Frullania*-type branches (F), with 3–4-fid first branch underleaves (UL¹) (×34; 1 mm scale). **2, 3.** Two leaves (×47; 600 µm scale). **4.** Three underleaves (×47; 600 µm scale). **5, 6.** Lobes of underleaves (×150; 150 µm scale). **7.** Leaf (×47; 600 µm scale). **8.** Stem half-leaf (×47; 600 µm scale). **9.** Stem underleaf (×47; 600 µm scale). **10.** Branch underleaf (×47; 600 µm scale). **11.** Stem cross section (×150; 150 µm scale at right). **12–14.** Cells of leaf lobe (12), middle (13) and leaf base (14) (×265; 100 µm scale). **15.** Leaf (×265; 600 µm scale). (All from *Schuster 95-1435,* New Zealand.)

←

ventral merophyte width of 10 cells. **12.** Outline of plant at low magnification. (Figs. 1, 4, 7, 11 from *Engel 23201,* New Zealand, South Is., Southland Prov., immediately N of Ten Mile Bush, near W shore of Lake Te Anau; remainder from *Child 4373,* New Zealand, South Is., Marlborough Prov., Red Hills.)

River, head of Lake Wakatipu, vicinity of Paradise, ca. 365–455 m, *Child 2421, 2467B* (F); Paradise, Dart Valley, N of N end Lake Wakatipu, ca. 365 m, *Child 1197* (F). OTAGO/WESTLAND PROV. BOUNDARY: Haast Pass, *Matthews s. n.* (Allison H3158) (F); Haast Pass, ca. 610 m, *Child H4506* (F). WESTLAND PROV.: Camp Creek, W of Alexander Range, 210 m, *Reif C11Z* (F); Ahaura, ENE of Greymouth, ca. 150 m, *Child H3745* (F). MARLBOROUGH NEAR BOUNDRY WITH NELSON PROV.: Mt. Richmond Forest Park, Red Hills, track to Maitland Hut, NE of St. Arnaud, ca. 700–920 m, *Engel 21438* (F). MARLBOROUGH PROV.: Red Hills, W of hut ca. 915 m, *Child H4373* (F). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, ca. 7 km from Ohakune on Ohakune Mt. Road, 900 m, *Engel 22702* (F). GISBORNE PROV.: Urewera Natl. Park, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 650–920 m, *Engel 20588* (F). SOUTH AUCKLAND PROV.: Waiotapu, Rotorua, *Child 43C* (F).

Lepidozia laevifolia (Hook. f. & Tayl.) G. L. & N. Figures 20–22

Jungermannia laevifolia Hook. f. & Tayl., London J. Bot. 3: 385. 1844 (3: 285. [*sic*] *in errore pro* 385). *Lepidozia laevifolia* (Hook. f. & Tayl.) G. L. & N., Syn. Hep. 208. 1845. *Mastigophora laevifolia* (Hook. f. & Tayl.) Trev., Cat. Herb. Crypt. Trevisan 2: 30. 1853. Lectotype (*nov.*): Campbell Is., Nov. 1840, *Hooker* (FH!).

Lepidozia minuta Col., Trans. & Proc. New Zealand Inst. 18: 245. 1886 *non L. minuta* Steph., Spec. Hep. 3: 603. 1909. Original material: New Zealand, Waipawa Co., near Norsewood, 1885, *Colenso a. 1419* (BM!, G = 0, WELT!).

Lepidozia retrusa Col., Trans. & Proc. New Zealand Inst. 22: 455. 1890 (1889). Original material: New Zealand, Waipawa Co., S of Dannevirke, 1889, *Colenso a. 1515* (BM!—c. sporo., G = 0, WELT!—c. per.).

Lepidozia papillata Steph., Spec. Hep. 3: 595. 1909. Original material: Auckland Is., *Hooker* (G!, "sub *Lepid. dispar*").

Lepidozia asperifolia Steph., Spec. Hep. 3: 596. 1909. Original material: New Zealand, South Is. (*non vidi*).

Plants closely prostrate, flexuous, with spreading branches, green, nitid when dry, the shoots small, to 1 cm wide, including branches; exceptionally luxurient phases to 2.5 cm long × 0.9 cm wide. Branching nearly exclusively of *Frullania* type, rather short, normally irregularly and distantly pinnate, ± regularly pinnate in well-developed plants, the primary (and secondary) branches sometimes becoming whiplike, flagelliform and microphyllous, the nonmicrophyllous leaves ± symmetrically 4-lobed; primary branches occasionally developing into new leading shoots; secondary branches occasional, 1–4 per primary branch; branch half-leaf subsymmetrical, cordate, 2-lobed to ca. 0.25; first branch underleaf (1)2–4-lobed, inserted on ventral side of branch base to the ventral-lateral side of junction of main axis and branch, in both cases the first branch underleaf aligned with underleaves of branch. Ventral-intercalary branching occasional, leafy, at times becoming leading shoots. Stems flexuous, ca. 10 cells in diam., the cortical cells in 1 layer of thick-walled cells somewhat larger than the thick-walled medullary cells. Leaves when dry deeply cup-shaped, with the tips of the lobes incurved and not visible in dorsal view; leaves when moist rigid, distinctly concave, contiguous, with much of stem visible in dorsal view, 0.5–0.65 mm long at longest point, 0.5–0.7 mm wide at widest point, spreading, the insertion distinctly incubous; leaves variable, subsymmetrical to distinctly asymmetrical, subequally 4(6)-lobed, sometimes with a ± shallow dorsal sinus, the leaves divided to ca. 0.4–0.65 (median sinus), the distance from dorsal sinus base to insertion ± equal to or much greater than that from ventral sinus to insertion. Lobes broadly to narrowly acute, sometimes short-apiculate, the two ventral occasionally somewhat divergent from the dorsal lobes, the lobe margins entire to somewhat sinuate to occasionally 1–2-dentate, terminating in a single cell or a uniseriate row of 2–3 nonelongated, thick-walled cells; dorsal lobe 5–10 cells wide at base (at times 4 cells wide in minute phases). Disc subsymmetrical to asymmetrical and then obliquely truncate, 12–18 cells high at dorsal sinus, 4–9 cells high at ventral sinus; dorsal margin ampliate, cordate to auriculate at the insertion (rarely decurrent), entire to sinuate, sometimes irregularly crenulate to dentate; ventral margin shorter than dorsal, ± cordate at the insertion, entire or sometimes with an accessory lobe. Cells evenly thick-walled, occasionally with small trigones, the cells of median portion of disc 16–25(28) μm wide × 19–32 μm long, ± longitudinally elongated, typically sharply differentiated from the small and isodiametric (8–10 μm) cells of the lobes and ampliate sector of the disc; marginal cells of disc and lobes lacking a thickened outer wall; cuticle of abaxial surface coarsely and closely papillose on lobes and ampliate sector (the adaxial surface typically smooth), the disc closely striate-papillose. Underleaves inserted on 6–8 rows of stem cells, spreading, short, broader than high, symmetrically 4-fid to ca. 0.3–0.45 (median sinus), the lobes plane, entire, acute to acuminate, terminating in a single cell or a uniseriate row of 2–4 cells; disc 7–8 cells

high at median sinus, cordate at the insertion, the margins plane, entire.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, sometimes cernuous ventral-intercalary branches from main shoot or terminal on long flagelliform primary branches; bracts ventricose–cucullate, 2-lobed to ca. 0.3–0.4, the lobes acute to apiculate, the lateral margins occasionally with several slime papillae; antheridia 1–2 per bract, the stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series much larger than leaves, erect and sheathing the perianth, the bracts deeply concave, suborbicular to broadly ovate to suboblate; apices with 4 small teeth hardly differentiated from the otherwise crenate-denticulate apex, or with (2)4 short, rather irregular lobes composed of ± regularly rectangular + irregularly and feebly sinuate-rhomboidal cells, the apical end of the marginal cells often feebly diverging, the lobes thus finely and sparingly crenulate; lamina composed of ± regularly short rectangular cells, the margin bordered by cells of variable shape, some hardly longer than wide, others rather long and narrow, the apical or free end of marginal cells variously divergent and forming a short projection or a tooth, the margin irregularly crenate-denticulate to the base, the teeth occasionally composed of a few to several cells; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth, the lobes composed of ± tiered, long, narrow, subrectangular cells; mouth cells rather thick-walled, at the apical end laterally free for varying lengths, the mouth thus crenate-denticulate; perianth cells ± regularly rather short to long subrectangular below mouth and here the cuticle is conspicuously striate-papillose; perianth 2-stratose near base.

Seta with 8 rows of outer cells surrounding an inner core of 18 much smaller cells. Capsule wall 30–35 μm thick, of 3–4 or 4–5 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheetlike thickenings alternating with those that are devoid of thickenings (or are rarely locally thickened), the transverse walls usually devoid of thickenings or sporadically have an isolated nodule; innermost layer of cells ± tiered, narrowly rectangular, with nodulelike to spinelike thickenings common, with semiannular bands weakly developed, only occasionally present, often incomplete, pale.

Spores 11.5–13.4 μm, exine light brown, with dense, rather coarse, sharply defined, rather broad papillae and simple or furcate vermiculate markings. Elaters ± rigid to feebly tortuous, 9.6–10.1 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 3.4–3.8 μm wide.

DIFFERENTIATION—Examination of the type of *Jungermannia laevifolia,* a Campbell Is. plant, reveals that the species is identical with the common New Zealand plant called *Lepidozia asperifolia* by Stephani (1909, sub *L. "levifolia"*), who maintained that the true *L. laevifolia* did not occur in New Zealand. Hodgson (1956) and others (e.g., Allison & Child, 1975) use the name *Lepidozia laevifolia* collectively to refer to all of the New Zealand species of the "laevifolia" complex. When differentiated, however, as they are here, the name must be applied to the plant with leaves densely papillose, and broadly ampliate dorsal margins. The species epithet, "*laevifolia,*" is unfortunate and misleading, standing in contradiction to the more appropriate names "papillata" and "asperifolia."

A note on the type of *Lepidozia papillata* (G!) indicates that the specimen was extracted from a specimen of *Lepidozia dispar* (= *Kurzia hippuroides*), leg. Hooker on Auckland Is., Herb. Kew. At least one of the specimens labeled *L. dispar* at BM includes strands of *Lepidozia laevifolia,* but other liverwort species that are associated with the type of *L. papillata* at G are not present, and this element in the BM specimen cannot be confidently regarded as an isotype of *L. papillata.*

Stephani (1892) referred *L. minuta* Col. and *L. retrusa* Col. to *L. praenitens* (= *Telaranea praenitens* (Lehm. & Lindenb.) Hodg.). The types of these two Colenso species (BM!) were annotated by Stephani as *L. praenitens*; both are *Lepidozia laevifolia.*

Small, poorly developed plants of *L. laevifolia* and *L. pumila* may be difficult to distinguish satisfactorily. Both species can have distinctly concave leaves with the lobes incurved and hidden when viewed in dorsal aspect. Well-developed leaves should always be selected for examination, but a number of leaves should also be examined to determine the range of variation. The leaves of *L. laevifolia* are nearly always coarsely papillose (Fig. 20 : 8–10), and the papillae are typically present only on the abaxial surface of the leaf (the adaxial surface being almost smooth). Distinctly

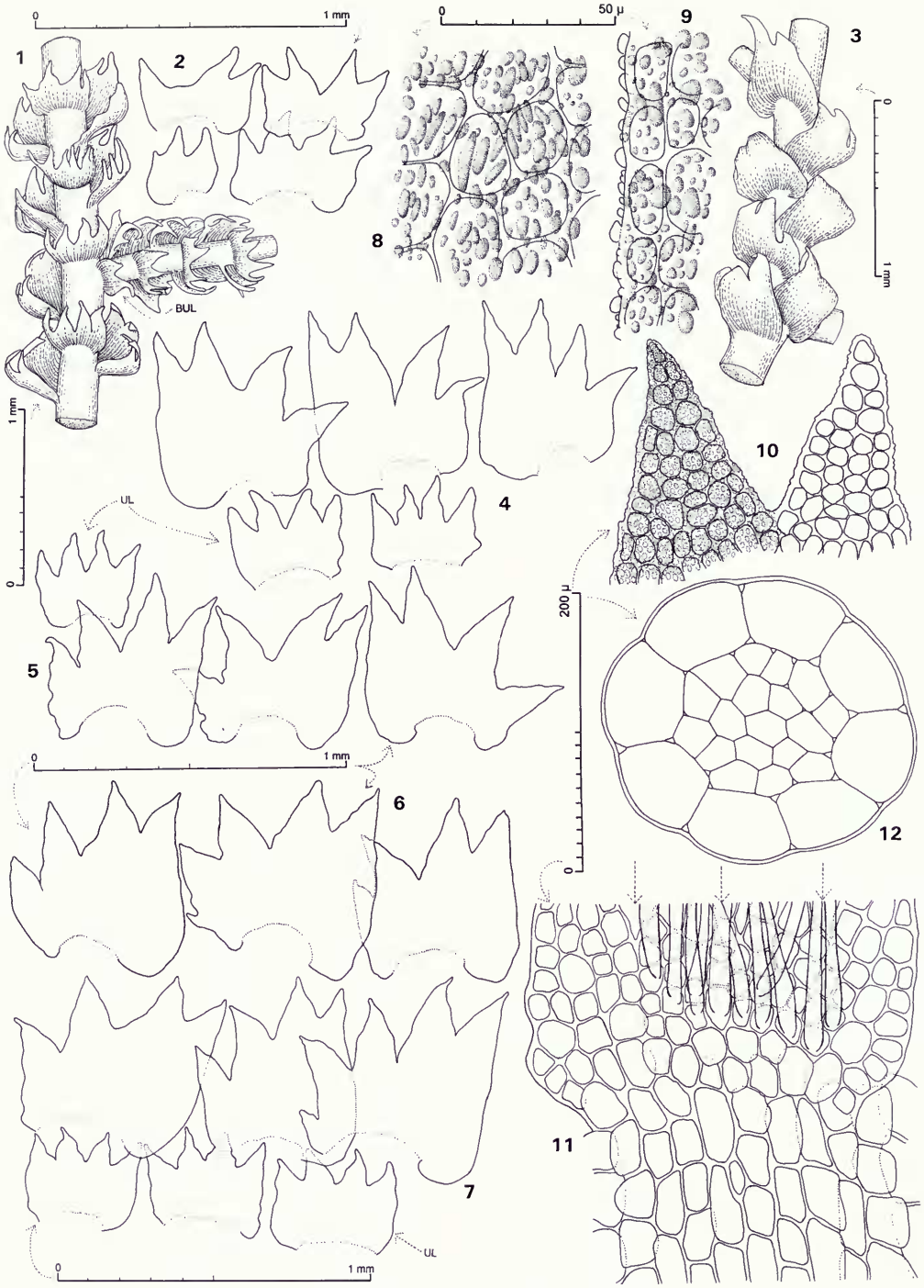

FIG. 20. *Lepidozia laevifolia* (Hook. f. & Tayl.) G. L. & N. (Figs. 6, 7 from var. *acutiloba*; remainder from var. *laevifolia*). **1.** Sector of main shoot with *Frullania*-type branch, ventral view (BUL, first branch underleaf). **2.** First branch underleaves. **3.** Sector of shoot, dorsal view. **4–7.** Leaves and underleaves (ul), all drawn at same scale. **8.** Median disc cells showing cuticular papillae. **9.** Marginal cells of ampliate sector of disc. **10.** Leaf lobes showing cuticular papillae in lobe at left. **11.** Portion of stem with underleaf disc and lobe bases. Note ventral merophyte width of 10 cells and rhizoid origin (arrows indicate sinus bases). **12.** Seta, cross section. (Figs. 1–3 from *Engel*

papillose leaves may vary vis-à-vis the number of papillae per cell: Some populations have very coarse papillae that number ca. 7–8 or 12–15 per cell (as in the type of *L. laevifolia,* Fig. 20 : 8). Other populations are less coursely papillose, with ca. 30 papillae per cell. The dorsal leaf margin in *L. laevifolia* is usually ampliate and distinctly cordate at the insertion, the margins of the disc and lobes are sinuate, and the cells of the ampliate portion are small and abruptly differentiated from the cells of the disc. Typically, in *L. pumila* the cuticle is smooth, and the dorsal leaf margin is straight and abruptly cordate at the base (Fig. 29 : 1, 4, 5); the leaf cells appear large in proportion to the size of the leaf, giving the leaf a "cellular" appearance. Another useful character in distinguishing *L. pumila* from *L. laevifolia* is the presence in the former species of a thickened outer wall of at least some of the marginal cells of disc and lobes (Fig. 29 : 6, 8).

Suboptimal phases of *L. laevifolia* at times have mostly undivided first branch underleaves and therefore may be confused with *L. acantha.* Such populations differ from *L. acantha* by the non-elongated cells of the leaf lobe uniseriate row, the arched dorsal margin of the leaf disc, and the presence of at least some bifid (or trifid) first branch underleaves. Bilobed first branch underleaves in *L. acantha* are very rare. It is important to select the best-developed shoots when examining suspected suboptimal populations.

In the dilated dorsal leaf bases similar to *L. elobata,* which differs in the consistently unlobed first branch underleaves (Fig. 28 : 1); the relatively narrower leaves (Fig. 28 : 3, 4, 8); and the shallower median sinus of the leaf (Fig. 28 : 3, 4, 7–8).

The species is separable into three varieties, as follows.

Key to the varieties of *L. laevifolia*

1. Dorsal half of leaf more deeply bilobed (typically to 0.2 or more); disc cells moderately and evenly thick-walled, occasionally with small trigones 2
2. Leaf lobes narrowly acute, the two dorsal lobes separated by a narrow, rather deep sinus (less than 45°); median disc cells large, 18–25(28) μm wide; leaf margins sinuate to occasionally 1–2-dentate; underleaf lobes slenderly acuminate; leaves ± strongly asymmetrical. Occurring from (60 m) 300 m to subalpine zone ..... var. *laevifolia*
2. Leaf lobes broadly acute, the two dorsal lobes separated by a broad, shallow sinus (45–90°); median disc cells narrow, 16–20 μm wide; leaf margins often sinuate, never toothed; underleaf lobes acute to broadly acuminate; leaves weakly asymmetrical. Occurring in upper-elevation forests to alpine zone ..... var. *acutiloba*

1. Dorsal half of leaf very shallowly bilobed (to 0.15–0.2); disc cells evenly and very strongly thick-walled, no trigones ..... var. *alpina*

Lepidozia laevifolia* var. *laevifolia

Leaves ± strongly asymmetrical, obliquely truncate, 4(6)-lobed, divided to 0.5–0.65 (median sinus); leaf lobes narrowly acute, the two dorsal lobes ± paired, separated by a narrow, rather deep sinus (less than 45°); disc 12–15 cells high at dorsal sinus, 4–7 cells high at ventral sinus, the ventral sinus often ± reflexed; leaf margins occasionally 1–2-dentate; median disc cells 18–25(28) μm wide; underleaf lobes slenderly acuminate, at times only 2–3 cells wide at base.

DISTRIBUTION–ECOLOGY—Amphipacific temperate: Macquarie Is., Auckland and Campbell Is., New Zealand (South Is., North Is.), Tasmania, Australia (Victoria, N.S.W.), Kerguelen Is., Marion and Prince Edward Is., Falkland Is., southern South America, Juan Fernandez Is.

In New Zealand var. *laevifolia* typically ranges from middle-elevation forests to the subalpine zone and is able to tolerate considerable exposure. However, it may be present in lower-elevation forests, and it extends as far north as Radar Bush (WSW of Cape Reinga), where it occurs on rotted, decorticated logs in forests of *Beilschmiedia–Vitex–Hoheria* and *Cyathea dealbata* (100 m).

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18406, New Zealand, South Is., Arthur's Pass Natl. Park, Kelly Range; 4, 8–10 from type of *L. laevifolia*; 5 from *Engel 20585,* New Zealand, North Is., Gisborne Prov., Urewera Natl. Park, Waikareiti Track; 6 from *Engel 22816,* South Is., Nelson Prov., road to Rainbow Skifield in vicinity of Red Gate, just W of Wairau River; 7 from type of var. *acutiloba*; 11 from *Engel 22885,* New Zealand, South Is., Westland/Canterbury Prov. Boundary, Arthur's Pass Natl. Park, Bealey Valley Track; 12 from *Child 2849,* New Zealand, South Is., Otago Prov., Maungatua.)

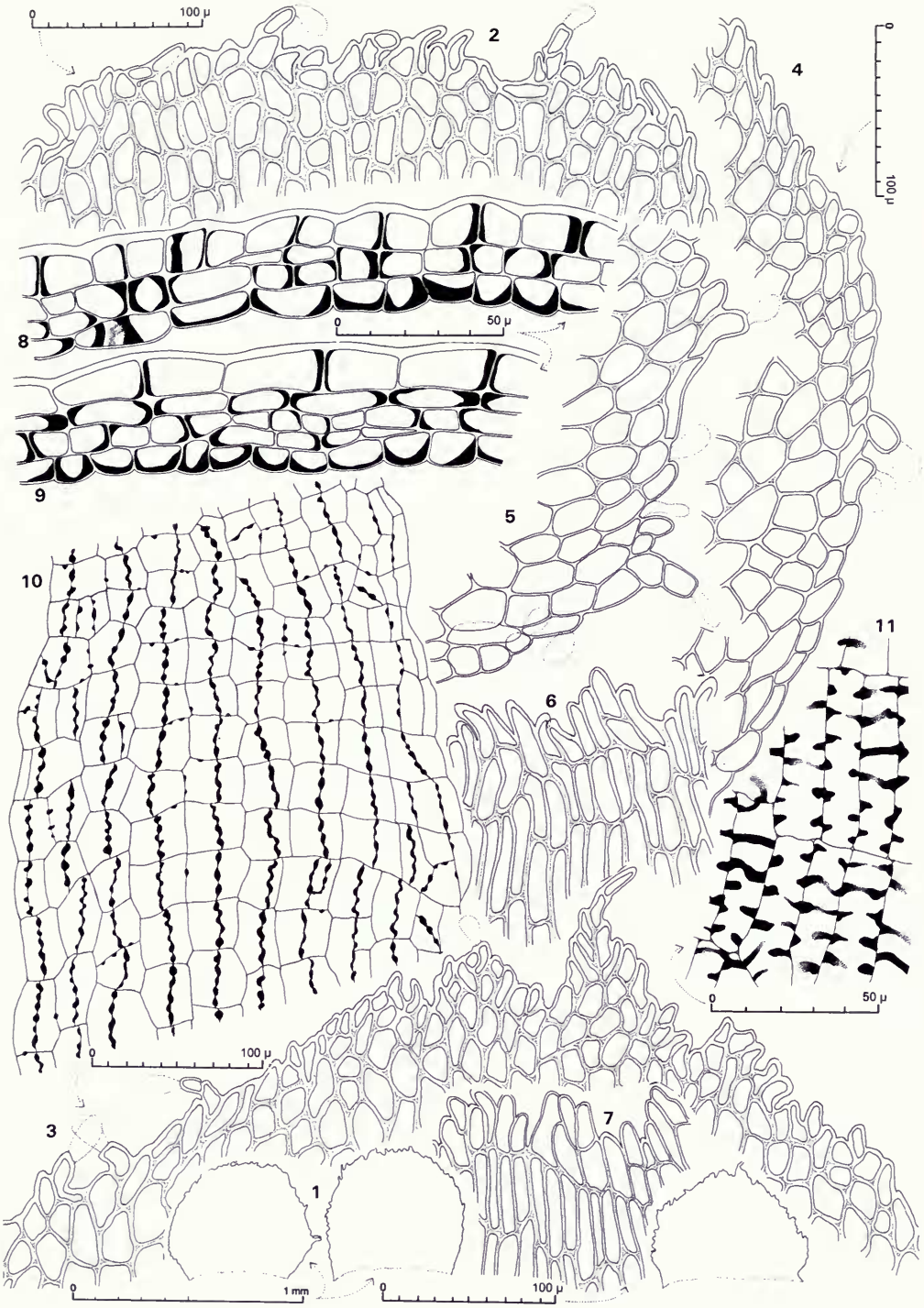

FIG. 21. *Lepidozia laevifolia* (Hook. f. & Tayl.) G. L. & N. **1.** Two bracts and (to right) bracteole from innermost series (all drawn to same scale). **2, 3.** Portions of apex of 2 innermost bracts. **4, 5.** Complete lateral margin and basal half of margin, respectively, of innermost bracts (drawn to same scale). **6, 7.** Portions of perianth mouth (drawn to same scale). **8, 9.** Capsule, cross sections of 3–4- and 4–5-stratose walls. **10.** Capsule wall, outer layer. **11.** Capsule wall, inner layer. (All from *Engel 20669,* New Zealand, North Is., near Gisborne/South Auckland Prov. Boundary, Urewera Natl. Park, crest trail from Highway 38 towards Whakataka summit.)

Also present at ca. 60–80 m in the Kiwanis Reserve (S of Kaitaia), where it occurs on nikau in mixed broadleaf forests dominated by *Beilschmiedia* and *Vitex*, with *Rhopalostylis* (nikau), *Coprosma, Dacrycarpus,* and *Hoheria.* Generally, however, the variety is less common below 300 m. In forests it occurs on shaded, moist cliff faces and boulders, soil banks (including banks of roadcuts through the forest, and here at times mixed with *Breutelia elongata*), rotted logs, and occasionally over bark. It is rather common on the floor and loosely on bark at the bases of *Leptospermum* in the "Frost Flats" (South Auckland Prov., near Otupaka Stream, SW of Minginui). In subalpine situations it occurs on soil under and in between tussocks (at times where the tussock base is rotted), under shrub cover, in boulder fields, on cliff faces (where it sometimes forms sheets) and on clayey banks. In boggy sites, it may occur among *Sphagnum,* and then the shoots are often quite straggly.

SELECTED SPECIMENS SEEN—CAMPBELL IS.: *Kirk 314,* syntype of *L. novae-zelandiae*—c. sporo. (G). NEW ZEALAND. SOUTH ISLAND. SOUTHLAND: Fiordland Natl. Park, Borland Road, 14 km by road WNW from Borland Lodge, near South Branch of Borland Burn, 855–870 m, *Engel 18687* (F); East Dome, Garvie Range, ca. 1370 m, *Child H3913* (F); Wilmot Pass Road to Deep Cove, ca. 305 m, *Child H5602* as *L. microphylla* (F). OTAGO PROV.: Ajax Swamp, ca. 1 km N of Ajax Hill, Catlins River area, ca. 610 m, *Child H5492* (F); Mt. Maungatua, W of Mosgiel, ca. 500 m, *Engel 17781* (F); Maungatua, W of Mosgiel, ca. 855 m, *Child H140* as *L. microphylla* (F); Silverpeaks, N of Dunedin, ca. 455 m, *Child H3406* (F); Flagstaff, NW of Dunedin, ca. 455 m, *Child 1377* as *L. microphylla* (F); Lammermoor Range, ca. 610 m, *Child H3843* (F); Great Moss Swamp, WSW of Middlemarch, ca. 305 m, *Child H472* (F); Kakanui Range, ca. 1220 m, *Child H2837* (F). WESTLAND PROV.: Near Hercules Creek on Route 6 in Mt. Hercules Scenic Reserve, *Engel 6559* (F); upper Otira Valley, ca. 1220 m, *Child H5342* (F); Arthur's Pass Natl. Park, Kelly Range, off track to Carroll Hut, above Kellys Creek, N of Otira, 1040–1110 m, *Engel 18406* (F); Camp Creek, W of Alexander Range, 320 m, *Reif C29C* (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Arthur's Pass, near Temple Basin Ski area, *Engel 6473A* (F); ibid., Dobson Nature Walk, summit area of Arthur's Pass, 920 m, *Engel 22025* (F); ibid., Bealey Valley Track, ca. 875–900 m, *Engel 22885* (F). CANTERBURY PROV.: Mt. Cook Natl. Park, Governors Bush, SW of town of Mt. Cook, 760–800 m, *Engel 18206*—c. per. (F); Arthur's Pass Natl. Park, immediately below Punchbowl Falls, *Engel 6870* (F); Mt. Gloriana, Spencer Range, 1676 m, *Child H 3965B* (F); Mt. Tourlesse, *Hatcher 1221* (F). NELSON PROV.: Nelson Lakes Natl. Park, Pinchgut Track, W of southern sector of Lake Rotoiti, SSW of St. Arnaud, ca. 1280–1390 m, *Engel 21405* (F); ibid., NE margin of Lake Rotoroa, W of St. Arnaud, 520 m, *Engel 21505* (F). MARLBOROUGH NEAR BOUNDRY WITH NELSON PROV.: Mt. Richmond Forest Park, Red Hills, track to Maitland Hut, NE of St. Arnaud, ca. 700–920 m, *Engel 21472* (F). NORTH ISLAND. Without specific locality, "alpine interior," *Colenso a.2200* as *L. praeniiens* (BM). WELLINGTON PROV.: Near eastern border of Tongariro Natl. Park along road to Tree Trunk Gorge, ca. 0.5 km W from gorge, 750 m, *Engel 21209* (F). GISBORNE PROV.: Urewera Natl. Park, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 650–920 m, *Engel 20585* (F). NEAR GISBORNE/SOUTH AUCKLAND PROV. BOUNDARY: Urewera Natl. Park, crest trail from highway 38 toward Whakataka summit, N of northern extremity of Lake Waikaremoana, 930–1030 m, *Engel 20669*—c. sporo. (F). SOUTH AUCKLAND PROV.: "Frost Flats," on South Road between Totara Salvage Road and Wong Road, near Otupaka Stream, SW of Minginui, *Engel 20747* (F); Whirinaki Forest Park, Waterfall Loop track, near Whirinaki River, SSW of Minginui, *Engel 20694* (F); Rotorua thermal area, *Hatcher 90* (F); 7 km N of junction of Highways 33 and 30 on Highway 30, *Kantak & Churchill 78*—c. ♂ (F). NORTH AUCKLAND PROV.: Auckland, *Cheeseman 32,* syntype of *L. novae-zelandiae* (G); NE Waitakere Ranges, Swanson University Reserve, Tram Valley Road, 95 m, *Engel 20466*—c. per. (F); same loc., *Braggins 99/275* (AKU); SE corner of Waipoua Forest, just N of Tutamoe, 540 m, *Engel 21118* (F); Mangamuka Walkway, Maungataniwha Range, ESE of Kaitaia, saddle on State Highway 1, 390 m, *Engel 20960* (F); Kiwanis Reserve, junction of Okahu Stream and unnamed stream, ca. 5 km S of Kaitaia, N edge of Herekino Forest area, S of Quarry, ca. 60–80 m, *Engel 20907* (F); Radar Bush, WSW of Cape Reinga, S of Mt. Te Paki, ca. 100 m, *Engel 20850* (F).

Lepidozia laevifolia var. ***acutiloba*** Engel, var. nov.

Lobi foliares late acuti, sinu inter lobos dorsales duos non profundo, lato (45–90°) instructi; cellulae medianae disci angustae 16–20 μm latae; lobi amphigastrii acuti vel late acuminati.

HOLOTYPE—New Zealand, South Is., Otago Prov., W slope of Flagstaff, NW of Dunedin, 560 m, *Engel 17632* (F); isotype: (CHR).

Leaves weakly asymmetrical, ± equally 4(6)-lobed, divided to 0.35–0.5 (median sinus); leaf lobes broadly acute, the two dorsal lobes separated by a broad, often shallow sinus (45–90°), the disc 16–19 cells high at dorsal sinus, 6–10 cells high at ventral sinus; leaf margins often sinuate but rarely toothed; median disc cells small, 16–20 μm wide; underleaves shallowly lobed, the lobes acute to broadly acuminate.

DISTRIBUTION–ECOLOGY—New Zealand (South Is., North Is.). Typically an upper-elevation plant,

occurring in the scrub *Nothofagus menziesii* transition zone and extending into the subalpine and alpine zones. It occurs on damp ground, sometimes appearing as a pioneer, at other times between tussocks or over leaf litter under shrubs; also on damp cliff faces, rock outcrops, and in rock crevices. In the forest zone it may be terricolous or corticolous, as well as occurring on rotted logs, particularly where there has been soil accumulation.

SELECTED SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: East Dome, Garvie Range, ca. 1370 m, *Child H 3910* (F). OTAGO PROV.: Rock & Pillar, S end, near McPhees Rock, WNW of Middlemarch, ca. 1220 m, *Child H3861* (F); Mt. Maungatua, W of Mosgiel, 760 m, *Engel 17766* (F); W slope of Flagstaff, NW of Dunedin, 560 m, *Engel 17632* (F); S side of Mt. Cargill, just below summit, N of Dunedin, ca. 670 m, *Engel 17578* (F); Kakanui Range, ridge to Kakanui Peak, ca. 1220 m, *Child H2838* (F); opposite Siberia Hut, WNW of Makarora, ca. 1065 m, *Child H2919* (F); Fiordland Natl. Park, near McKerrow Hut, head of Lake McKerrow, *Hatcher 1768* (F); ibid., Martin's Bay, N of McKerrow River, *Hatcher 844* (F). WESTLAND PROV.: Mt. Aspiring Natl. Park, below and W of Mt. Armstrong, SSW of Mt. Brewster, 1250–1450 m, *Engel 17792* (F); road to Rainbow Skifield in vicinity of Red Gate, just W of Wairau River, E of N end of Lake Rotoiti, 700 m, *Engel 22816* (F). CANTERBURY PROV.: Mt. Cook Natl. Park, SW facing cliffs off Wakefield Track, overlooking Hooker River, E of town of Mt. Cook, 720 m, *Engel 18177* (F); ibid., Stocking Stream, SW facing cliffs above Hooker Valley, 1280–1330 m, *Engel 18244* (F); Arthur's Pass Natl. Park, immediately below Punchbowl Falls, *Engel 6896* (F); ibid., near start of Punchbowl Creek Track just above village of Arthur's Pass, *Engel 6913* (F); junction of Craigieburn River and Route 73, *Engel 6922* (F). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, track to Soda Springs, along Mangatepopo Stream, ca. 1300 m, *Engel 22499* (F); ibid., Blyth Track, along small stream ca. 0.5 km from Ohakune Mt. Road, ca. 1230 m, *Engel 21302* (F). GISBORNE PROV.: Urewera Natl. Park, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 650–920 m, *Engel 20552* (F).

Lepidozia laevifolia var. ***alpina*** Schust. & Engel, var. nov.

Dimidium folii dorsale non profunde bilobum, usque 0.15-0.2 longitudinis folii; cellulae disci parietibus aequaliter atque pervalde incrassatis praeditae, trigonis carentes.

HOLOTYPE—New Zealand, South Is., Fiordland Natl. Park, Gertrude Cirque NE of Homer Tunnel, below saddle on W facing exposed cliff, 1945 m, *Schuster 95-2089* (hb. Schuster).

Plants 500–550 to 760–810 μm broad with leaves, rather remotely pinnate, the branches in small part becoming flagelliform, rhizoidous; leaves strongly asymetrically bifid, with each lobe again bifid, ca. 380–420 μm broad × 440–480(500) μm long; dorsal half of leaf much larger and longer than ventral half, ca. 0.15–0.2(0.25) bilobed, the lobes acute but not strongly so, ending in 2–3 subisodiametric or isodiametric cells; cells of disc strongly and evenly thick-walled, trigones lacking, the median disc cells (18)20–26 μm wide; cuticle papillose (at times obscurely so).

The var. *alpina* is similar to var. *acutiloba,* also of higher elevations, in the shallow dorsalmost sinus and the broadly acute lobes. The var. *alpina* differs from var. *acutiloba* in the exceptionally shallow dorsalmost sinus, in the exceedingly thick-walled leaf cells, and in the somewhat larger median disc cells ([18]20–26 μm wide versus 16–20 μm in var. *acutiloba*). Also, in var. *alpina* the dorsalmost sinus tends to be narrower than in var. *acutiloba* and may even be slitlike.

Variety *alpina* has distinctly thick-walled cells reminiscent of *L. pumila.* However, the var. *alpina* has shorter and much less tapered dorsal leaf lobes, separated by a rather shallow sinus. Also, unlike in *L. pumila,* the sinus separating the two dorsal lobes is usually much shallower than that separating the two ventral lobes. In *L. pumila* the dorsal sinus descends ca. 0.3–0.35 the leaf length, in var. *alpina* only about (0.15)0.2–0.25 the leaf length. Moreover, *L. pumila* lacks an auriculate dorsal leaf base, has larger disc cells (to 33 μm wide vs. at most 26 μm wide in var. *alpina*), and has ventral merophytes 5–6 cells wide versus 6–8 cells wide in var. *alpina.*

In leaf shape (particularly in the shallow dorsal sinus and cordate to cordate-auriculate dorsal bases) the variety is similar to *L. obtusiloba. Lepidozia obtusiloba,* however, has leaf and underleaf lobes usually blunt; they are always sharp in var. *alpina* (Fig. 22 : 1–8). Moreover, *L. obtusiloba* has leaves with a much deeper ventral sinus than in var. *alpina.*

The var. *alpina,* as the name implies, is an alpine plant, known only from ca. 1950 m. It is possible that var. *alpina* is a mere alpine extreme in which, with extreme exposure, the dorsal leaf lobes are abbreviated. Other characters of var. *alpina* relevant to extreme exposure are the very thick-walled leaf cells and the markedly thick cuticle.

Leaf surface ornamentation in this species is variable. It may be distinctly papillose on some shoots or obscurely so on others.

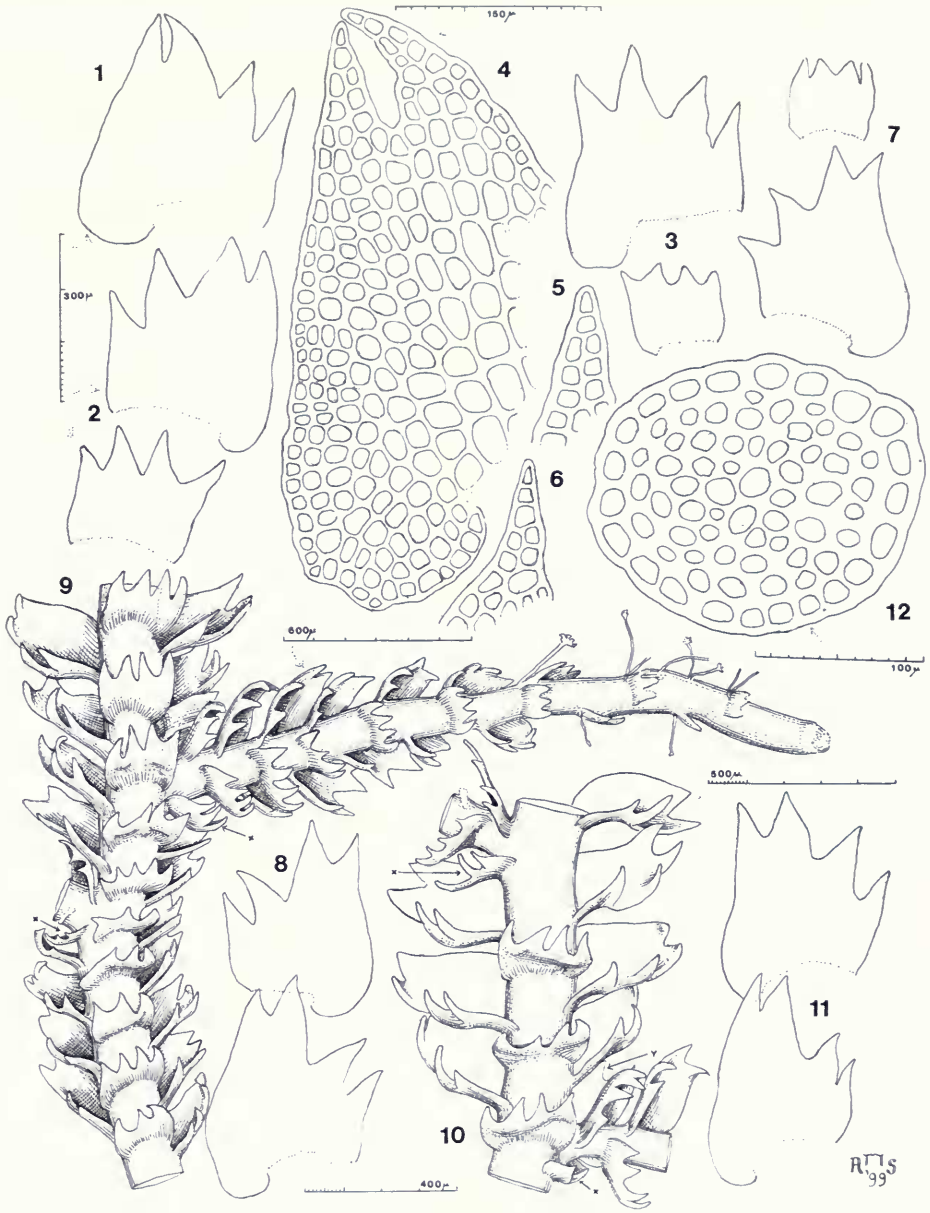

FIG. 22. *Lepidozia laevifolia* var. *alpina* Schust. & Engel. **1, 2.** Leaf and underleaves, main stem (×75; 300 μm scale). **3.** Leaf and underleaf, main stem (×75; 300 μm scale). **4.** Ventral half of leaf from Fig. 1 (×183; 150 μm scale). **5, 6.** Apices of dorsalmost lobe (×183; 150 μm scale). **7.** Leaf and underleaf (×51; 400 μm scale). **8.** Two large stem leaves (×51; 400 μm scale). **9.** Part of main axis with bases of two branches; note trifid basal branch underleaves (UL^1) (×42; 600 μm scale). **10.** Shoot sector, ventral aspect, with bases of two *Frullania*-type branches at UL^1, basal branch underleaves, at HL, part of stem half-leaf visible (×51; 500 μm scale). **11.** Two leaves (×51; 400 μm scale). **12.** Stem cross section (×225; 100 μm scale). (All from type.)

DISTRIBUTION–ECOLOGY—Known only from type plants, which occurred admixed with *Herbertus alpinus* and *Gymnomitrion strictum*, creeping amid *Hymenophyllum*.

Lepidozia fugax Engel, sp. nov. Figure 23.

Plantae in aspectu laceratae; apices lobi foliaris caduci e cellulis turgidis doliiformibus subisodiametrae con-

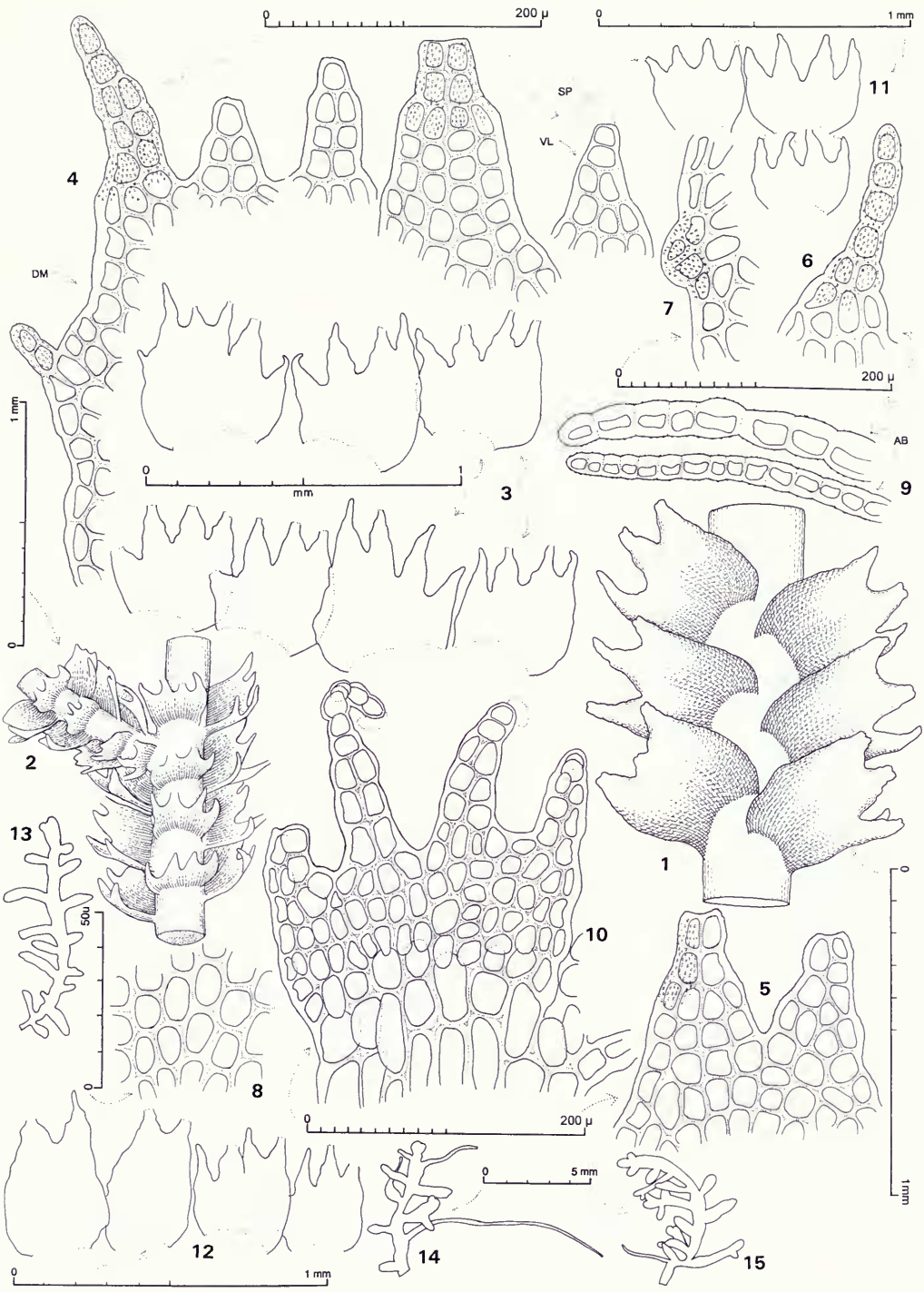

FIG. 23. *Lepidozia fugax* Engel. **1.** Sector of main shoot, dorsal view. **2.** Sector of main shoot and *Frullania*-type branch, ventral view. **3.** Leaves (note missing lobe tips). **4.** Dorsal margin of leaf (dm) and (left to right, i.e., dorsal to ventral) all lobes of same leaf (vl = ventral lobe; sp = slime papilla; cuticular papillae shown in part). **5.** Dorsal pair of lobes, the uniseriate sectors of each lobe having fallen away (cuticular papillae shown in part). **6.** Second dorsal lobe (complete; note constricted septa). **7.** Sector of dorsal margin of disc with a blunt tooth (cuticular papillae shown in part). **8.** Median disc cells of leaf. **9.** Leaf disc cross section (ab = abaxial face). **10.** Portion of stem with

stricto-septatis instructi; amphigastria in seriebus septem cellularum caulinarum inserta.

HOLOTYPE—New Zealand, South Is., Otago/Westland Prov. boundary: Mt. Aspiring Natl. Park, summit area of Haast Pass, 570 m, *Engel 18023* (F); isotype: (CHR).

Plants loosely prostrate, in pure mats, rather stiff and wiry, with spreading branches, green, distinctly nitid when dry, the shoots small, to 1.2 cm wide, including branches (shoots with rigorous branches), shoots with short branches at times only 3 mm wide. Branching nearly exclusively of *Frullania* type, short to rather long, irregularly 1(2)-pinnate, the primary (and secondary) branches sporadically to frequently becoming whiplike, flagelliform and microphyllous, the nonmicrophyllous leaves asymmetrically to subsymmetrically 4-lobed, the uniseriate portion submoniliform; primary branches occasionally developing into new leading shoots; secondary branches occasional, up to 6 per primary branch; branch half-leaf subsymmetrical, the basal sector somewhat rounded to subcordate, 2-lobed to ca. 0.3; first branch underleaf 2–3-lobed, inserted on ventral side of branch base to the ventral-lateral side of junction of main axis and branch, and in both cases, the first branch underleaf ± aligned with underleaves of branch. Ventral-intercalary branching occasional, leafy. Stems rather stiff. Leaves fragile and easily detached; when dry moderately concave, the dorsal lobes stiffly spreading, the tips of the ventral lobes usually incurved and not visible in dorsal view; leaves when moist often with a ragged appearance, slightly concave, contiguous to imbricate, with much of stem visible in dorsal view, 0.3–0.5 mm wide and long, distinctly spreading, the dorsal margin forming an angle with stem as much as ca. 90°, the insertion distinctly incubous; leaves variable in shape, subsymmetrical to moderately asymmetrical, subequally to unequally 4(5)-lobed, the leaves divided to ca. 0.3–0.5 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion. Lobes acuminate, often appearing short in proportion to disc, ± parallel to weakly divergent, the tips often caducous (lobes often lacking the uniseriate sector), the lobes often becoming slender and 2 cells wide for much of their length, the dorsal lobes 2–4 cells wide at the base; lobes entire, terminating in a uniseriate row of 2–4(5) at most somewhat elongated (to ca. 1.3:1) cells, the cells of uniseriate row turgid, barrel-shaped, the septa constricted, the terminal cell rounded at the tip; cuticle of lobes papillose. Disc moderately to distinctly asymmetrical (the disc then obliquely truncate), 9–13 cells high at dorsal sinus, 6–7 cells high at ventral sinus; dorsal margin moderately ampliate, cordate at the insertion, mostly entire to sinuate, sporadically with a 1–2-celled blunt or sharp tooth; ventral margin somewhat shorter than the dorsal, subcordate at the insertion, entire or sometimes with a single tooth. Cells of median portion of disc with walls uniformly rather strongly thickened, trigones lacking, the cells 17–24 μm wide × 20–31 μm long, ± longitudinally elongated; cells of ampliate sector ± isodiametric; marginal cells of disc and lobes in surface view with a strongly thickened free wall (the wall often crescentic and bulging into the cell lumen), the disc cells in cross section with crescentic thickenings of the abaxial wall; cuticle of disc smooth. Underleaves inserted on 7 rows of stem cells, strongly spreading, ca. 1.5–2× stem width, broader than high, symmetrically 4-fid to ca. 0.3–0.5 (median sinus), the sinuses V-shaped, the lobes slender, acuminate, entire, the tips often caducous, terminating in a single cell or a uniseriate row of 2–3 cells; disc 5–7 cells high at median sinus, the margins plane, entire.

Asexual reproduction by caducous tips of leaf lobes.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, cernuous ventral-intercalary branches from main shoot or submicrophyllous primary branches; bracts ventricose-cucullate, 2-lobed to ca. 0.3, the lobes acute to apiculate, the lobe tips complete, the lateral margins entire or with a tooth; antheridia 1 per bract, the stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem, the gynoecium base bulbous, fleshy, polystratose and rhizoidous; bracts of innermost series much larger than leaves, erect and sheathing the

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underleaf; note ventral merophyte width of 7 cells. **11.** Underleaves. **12.** Two half-leaves and (to right) 2 first branch underleaves. **13–15.** Outlines of three shoots at low magnification (all at same scale). (All from holotype.)

perianth, the bracts deeply concave, suborbicular to suboblate; apices with 4 small, rather irregular lobes that are often composed of a base of 2 tiers of cells that are irregularly quadrate to short-rectangular to sporadically rather long and narrowly subrectangular, the apical end of the marginal lobe cells often feebly diverging, the lobes thus often finely and sparingly crenulate, the lobes often terminating in a uniseriate row of 2 narrowly rectangular cells or 2 laterally juxtaposed cells; lamina composed of ± regularly quadrate to short subrectangular cells, those of the distal sector rather thick-walled, those of remainder of bract (particularly those in a large median-basal field) thin-walled, the margin bordered by cells of variable shape, some hardly longer than wide, others rather long, narrow, and at times ± sinuate-rhomboidal, the apical or free end of marginal cells at times divergent and forming a short projection or a tooth, the margin irregularly crenate-denticulate in distal sector, the teeth unicellular or composed of a few cells but not forming a uniseriate row of 2 or more cells, the basal sector of bract margin entire except for slime papillae; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth, the lobes composed of ± tiered, long, narrow, subrectangular cells; mouth cells rather thick-walled, papillose, at the apical end laterally free for varying lengths, the mouth thus crenate-denticulate; perianth cells ± regularly rather short-subrectangular below mouth, and here the cuticle is conspicuously striate-papillose; perianth 2–3-stratose near base.

Seta with 8 rows of outer cells surrounding an inner core of numerous much smaller cells. Capsule oblong, the wall 26–30 μm thick, of 3 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheetlike thickenings and several large nodules alternating with those that are devoid of thickenings (or are sporadically locally thickened), the transverse walls usually devoid of thickenings or sporadically have a sheetlike thickening or an isolated nodule; innermost layer of cells narrowly rectangular, semiannular bands common, close and numerous, sometimes incomplete, rarely forked.

Spores 12.4–13 μm, exine brown, with coarse, sharply defined, close papillae and short vermiculate markings. Elaters rigid, nontortuous, 8.6–9.1 μm wide, only slightly and gradually tapering toward tips, bispiral to tips, the spirals 3.4–3.8 μm wide.

DIFFERENTIATION—The species is the only regional member of subg. *Notholepidozia* with caducuous leaf tips (Fig. 23 : 1, 3, 5), which give the plants a distinctive ragged appearance. The turgid, barrel-shaped cells of the uniseriate row and the constricted septa are responsible for the fragility of the lobes. The cells of the broken tips often have walls that have become secondarily thick-walled, rounded, and papillose, following the breakage of the lobe tips.

As in *Lepidozia novae-zelandiae,* the abaxial cell walls of the disc and lobes are strongly thickened, as confirmed by leaf cross sections (Fig. 23 : 9). These thickenings may also be viewed in a ventral aspect of the intact shoot by focusing on the ventral margins of the lobes. In surface view, only the outer wall of the marginal cells of disc and lobes appears thickened (Fig. 23 : 4).

DISTRIBUTION–ECOLOGY—Known only from two collections; the type occurred on an erect, decorticated, rotted, 30 foot high tree remnant in a *Nothofagus menziesii* forest at 570 m (Haast Pass). A second collection was made in the upper limits of a *Nothofagus menziesii* forest (900 m), where it occurred mixed with *Telaranea* cf. *corticola* on rotted wood at the base of a huge tree (Mt. Brewster).

SPECIMEN SEEN—NEW ZEALAND. SOUTH ISLAND. WESTLAND PROV.: Mt. Aspiring Natl. Park, off track to Mt. Brewster, below and W of Mt. Armstrong, SW of Mt. Brewster, ca. 900 m, *Engel 17847b* (F).

Lepidozia novae-zelandiae Steph. Figures 24; 25; 26: 4–13

Lepidozia novae-zelandiae Steph., Spec. Hep. 3: 595. 1909 ("Nova Zelandiae"). Lectotype (*nov.*): New Zealand, without specific locality, *Colenso 767* (G!)

Plants brittle, prostrate, in loosely interwoven, ± pure mats, the shoots slender, delicately spinescent, stiff and wirelike, with widely spreading branches, green, nitid when dry, the shoots minute, to 1.5 mm wide, including branches. Branching exclusively of *Frullania* type, ± distantly once-pinnate, the branches often becoming whiplike, flagelliform and microphyllous, the nonmicrophyllous leaves ± symmetrically 4-lobed; primary branches occasionally developing into new leading shoots; secondary branches spo-

radic, 1–2 per primary branch; branch half-leaf subsymmetrical, cordate at the base, 2-lobed to ca. 0.4; first branch underleaf (1) 2–3(4)-lobed, inserted on ventral side of branch base to the ventral–lateral side of junction of main axis and branch, nearly aligned with underleaves of branch. Ventral–intercalary branching not seen. Stems flexuous. Stem epidermal cells in surface view strongly thick-walled. Leaves when moist (or dry) moderately concave, with the lobes somewhat incurved, contiguous to ± distant, with much of stem visible in dorsal view, somewhat longer than wide, 0.25–0.3 mm long at longest point, 0.25–0.35 mm wide at widest point, spreading, the insertion subtransverse to weakly incubous; leaves variable, ± symmetrical to moderately asymmetrical, subequally 4(5)-lobed, the leaves divided to ca. 0.6 (median sinus), in ± symmetrical leaves the distance from dorsal sinus base to insertion not much greater than that from ventral sinus to insertion. Lobes longly acute to short-acuminate, typically somewhat apiculate, in asymmetrical leaves the dorsal lobes ± paired, the ventral shorter than the dorsal lobes and somewhat divergent, the dorsal lobes entire, 4–5 cells wide at base; lobes terminating in a single cell or in a uniseriate row of 2 cells, the cells of uniseriate row elongated (to 2:1), typically strongly thick-walled, the septa somewhat to distinctly dilated, the terminal cell tapering to a point; cuticle of abaxial surface of lobes coarsely papillose (the adaxial surface typically smooth). Disc subsymmetrical to obliquely truncate, 6–10 cells high at dorsal sinus, 4–6 cells high at ventral sinus, the margins entire, the dorsal margin ± straight, abruptly cordate near the base, entire to sinuate; ventral margin shorter than dorsal, at times distinctly so, entire or sinuate, sometimes with an accessory lobe. Cells of disc middle often strongly thick-walled, occasionally with small to medium trigones, 11–16 μm wide × 14–22 μm long; median basal cells in 1 (locally 2) rows of enlarged cells; marginal cells of disc and lobes with a strongly thickened, often concave outer wall (the wall thickening often crescentic and bulging into the cell lumen), the septa ± dilated; cuticle of disc finely to distinctly striate-papillose. Underleaves inserted on 4–6 rows of stem cells, spreading, symmetrically 4-fid to ca. 0.5 (median sinus), narrowing to the insertion, the lobes plane, slenderly acuminate, entire, terminating in a single cell or in a uniseriate row of 2–4(5) cells; disc 4–7 cells high at median sinus, the margins plane, entire. Cells of underleaf thicker-walled than those of leaves, similar in thickness to epidermal cells of stem.

Androecia and gynoecia not seen.

DIFFERENTIATION—*Lepidozia novae-zelandiae* is closely allied to *L. laevifolia,* as evidenced by the coarsely papillose leaves (Fig. 24 : 6), (the papillae are restricted to the abaxial leaf surface) and by the sinuate leaf margins. It differs in the subtransverse to weakly incubous leaf insertion (Fig. 24 : 2), the ± straight dorsal margin (Fig. 24 : 2–4), the strongly thickened outer walls and dilated septa of the marginal cells of both disc and lobes (Fig. 24 : 5–9), the elongated (to 2:1) cells of the uniseriate portion of the lobe apices (Fig. 24 : 5–8), and the distinctly thickened stem epidermal cell walls (Fig. 24 : 14–15). *Lepidozia pumila* resembles this species in the more or less straight dorsal margin of the leaves and thickened walls of the marginal cells, but the cuticle is typically smooth, and the leaves are more distinctly incubous.

In *L. novae-zelandiae,* the abaxial cell walls of disc and lobes are typically thickened; these thickenings can also be seen by focusing on the ventral margins of the lobes. Similarly thickened cell walls are present in *L. fugax* (Fig. 23 : 4, 9), but the characteristic deciduous lobe tips, and the barrel-shaped cells and constricted septa of the uniseriate row, will immediately distinguish that species from *L. novae-zelandiae.* It is notable that this species was known to Hodgson, as evidenced by a specimen (F!) identified as *L. novae-zelandiae;* she referred to this species (1956, p. 597 sub *L. laevifolia*) as "a form with many capillari-attenuated branches."

The subtransverse insertion of the leaves and the thick-walled, almost spinose terminal cells of the inflexed lobe tips of the main shoot and branches lend an aspect reminiscent of the genus *Psiloclada* Mitt. of the same family. The incrassate walls of the stem epidermal cells are similar to those of many *Kurzia* species.

Two of the syntypes of this species in Stephani's herbarium belong to *L. laevifolia:* Campbell Island, leg. Kirk, and New Zealand, Auckland, leg. Cheeseman. However, a syntype from Auckland Island, leg. Kirk, is *L. novae-zelandiae,* which establishes a rather wide-ranging distribution for this rare species.

VARIATION—Three extremes, evidently but not surely conspecific, are assigned to this species. The foregoing diagnosis and discussion apply

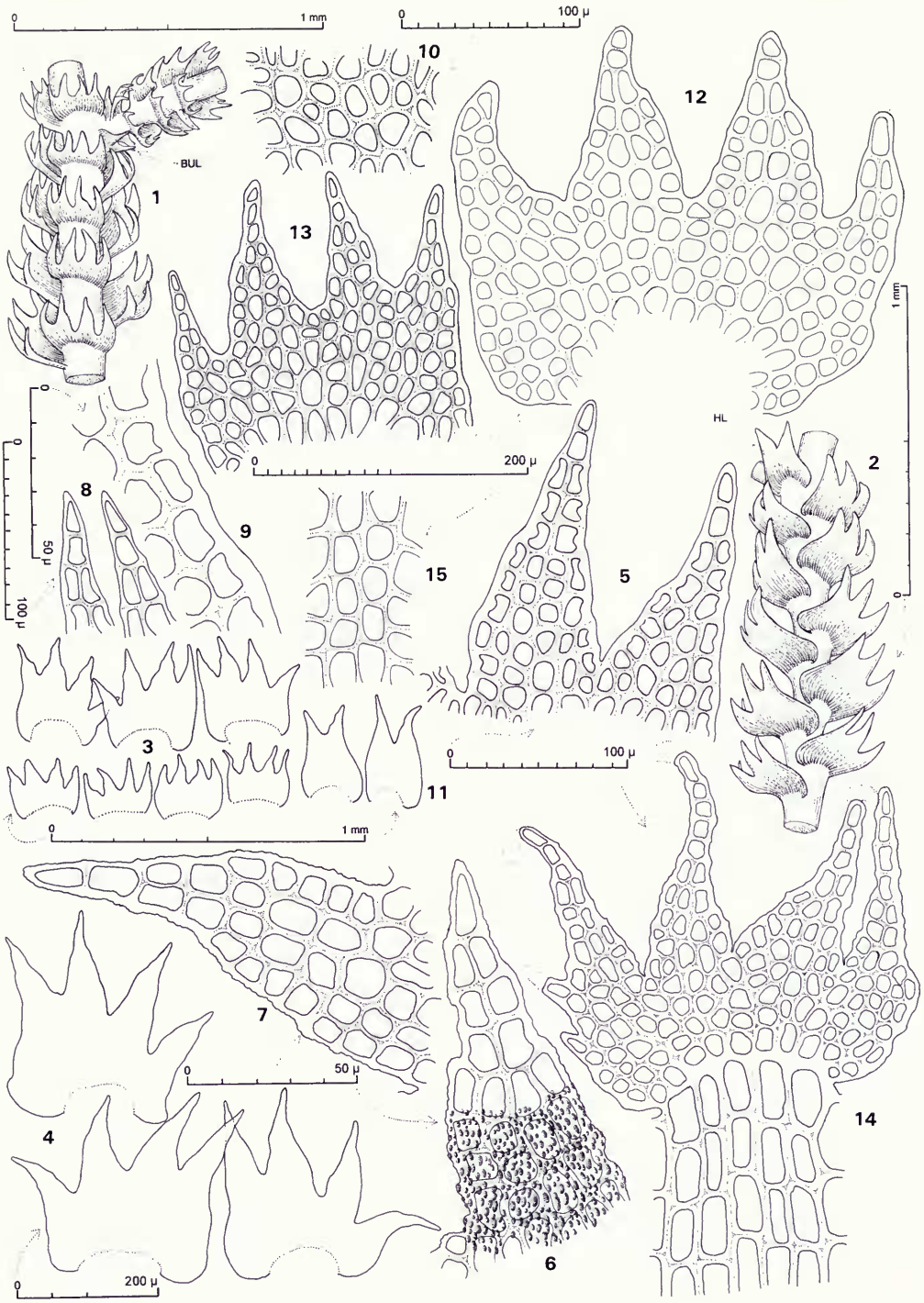

FIG. 24. *Lepidozia novae-zelandiae* Steph. **1.** Sector of main shoot, and *Frullania*-type branch, ventral view (BUL = first branch underleaf). **2.** Sector of main shoot (HL = half-leaf), dorsal view. **3.** Leaves; below, underleaves. **4.** Leaves. **5.** Dorsal leaf lobes. **6.** Dorsalmost leaf lobe, the cuticle indicated in part. **7.** Dorsalmost of median leaf lobes, cuticlar detail not shown. **8.** Distal sector of dorsal lobes. **9.** Portion of dorsal margin of leaf disc. **10.** Median cells of leaf disc. **11.** Two half-leaves. **12, 13.** Underleaves, cellular detail. **14.** Portion of stem with underleaf; note ventral merophyte width of 5 cells. **15.** Ventral cortical cells of stem, surface view. (Figs. 1–3, 5, 8–11, 13, 15 from *Schuster*

FIG. 25. *Lepidozia novae-zelandiae* var. *heterostipa* Schust. **1, 2.** Stem leaves, dorsal margin at left (×96; 150 μm scale). **3.** Dorsal lobe of leaf (×298; 80 μm scale). **4.** Dorsal lobes of leaf (×298; 80 μm scale). **5.** Dorsal half of leaf (×185; 150 μm scale). **6.** Leaf (×96; 150 μm scale). **7.** Underleaves (×96; 150 μm scale). **8, 8′,** and **8″.** Four sectors of a single stem showing 1- and 3-lobed basal branch underleaves (×85; 300 μm scale). **9, 9′,** and **9″.** Three sectors of one stem showing 1-, 2-, and 3-lobed basal branch underleaves (×85; 300 μm scale). **10, 11.** Leaves (×96; 150 μm scale). **12.** Shoot sector, dorsal aspect, at HL, half-leaves, at HUL[1], part of first branch underleaf visible (×85; 300 μm scale). (All from type.)

←

59645b, New Zealand, South Is., Westland Prov., upper reaches of Haast River, 0.6 mi. N of Haast Pass; 4, 6, 7, 14 from *Engel 23107,* New Zealand, South Is., Westland Prov., Mt. Aspiring Natl. Park, Cross Creek; 12 from *Hodgson s. n.,* New Zealand, North Is., Gisborne Prov., Lake Waikaremoana.)

solely to var. *novae-zelandiae.* The three differ as follows:

Key to the varieties of *L. novae-zelandiae*

1. Leaf lobes, excluding ventralmost, (3) 5–6 cells broad, to 7–9 cells long; basal branch underleaf (1)2–3(4)-lobed; underleaves with disc 4–5 cells high, the lobes 4–5 cells broad; underleaves inserted on 4–6 cell rows 2
   2. Dorsal leaf sinus descending ca. 0.35–0.4; ventral sinus descending usually over 0.5 the leaf length; dorsal and ventral sinuses usually wide open, V-shaped; leaf lobe apices ending in (1) 2 clearly elongated (to 2: 1) cells ..... var. *novae-zelandiae*
   2. Dorsal leaf sinus descending ca. 0.3–0.35 the leaf length; ventral sinus descending 0.45–0.5; dorsal (and often ventral) sinuses slitlike or narrowly V-shaped; leaf lobe apices ending in (1)2–3 subquadrate to short-triangular cells (1–1.5:1) ..... var. *heterostipa*
1. Leaf lobes 2–3 cells wide, 4–6 cells long; basal branch underleaf 1- or 2-lobed; underleaves with disc 2 cells high, the lobes usually few-celled, 2 cells broad at base; underleaves (8 cells broad at base) inserted on 4 cortical cell rows ..... var. *minima*

Lepidozia novae-zelandiae Steph. var. ***novae-zelandiae***

Distribution–Ecology—Aside from the type (of unknown provenance, but North Is. because it is a Colenso collection), this species is known from the Haast Pass area (Westland Prov.), Tongariro Natl. Park, Lake Waikaremoana, and the Waipoua area on North Island. Haast Pass collections were from steep, humid but never wet, shaded, vertical, south-facing cliffs in a *Nothofagus menziesii* forest, and may occur with *Plagiochila caducifolia, Gymnomitrion cuspidatum, Diplophyllum domesticum,* and *Radula* sp. The Tongariro National Park plant occurred within a mixed broadleaf forest (with *Nothofagus menziesii* common), and grew very loosely over soil on a vertical bank of the Mangawhero River. In the Waipoua area, the species occurred on a roadside bank under protected cover, with *Blechnum,* beneath a kauri forest.

Specimens Seen—AUCKLAND IS.: *Kirk s. n.,* syntype of *L. novae-zelandiae* (G). NEW ZEALAND. SOUTH ISLAND. WESTLAND PROV.: Upper reaches of Haast River, 0.6 mi. N of Haast Pass, ca. 520 m, *Schuster 53382a, 59645b* (F); Mt. Aspiring Natl. Park, Cross Creek, 1.1 km N of Haast Pass, 540 m, *Engel 21884* (F). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, Mangawhero River near juncture of Rimu Track and Forest Walk, just NE of Ohakune, 625 m, *Engel 22721* (F). GISBORNE PROV.: Lake Waikaremoana, 610 m, 1935, *Hodgson s. n.* (as *L. novae-zelandiae*) (F). NORTH AUCKLAND PROV.: Waipoua River, ca. 70 m upstream from State Highway 12 bridge, ca. 95 m, *Engel 21044* (F).

Lepidozia novae-zelandiae var. ***heterostipa*** Schust., var. nov.

Sinus folii dorsalis usque 0.3–0.35 longitudinis folii descendens, ventralis usque 0.45–0.5; sinus dorsalis atque saepe ventralis rimiformis vel in forma litterae 'V'; apices loborum foliarium in (1) 2–3 cellulas subquadratas vel brevi-triangulares terminantes.

Holotype—New Zealand, North Is., Tongariro Natl. Park, Tree Trunk Gorge, along west bank of Tongariro River, 15 Feb. 1995, *Schuster 95-772.*

Branching with strongly variable first branch underleaves; on one stem, primary underleaves 1-, 2-, and 3-lobed. Leaves usually strongly asymetrically quadrifid; dorsal lobes separated by a sinus descending usually (0.35) 0.4–0.45 the leaf length, the lobes narrow, usually 3–4 cells broad at base; dorsalmost sinus (between the two dorsal lobes) usually narrow, often slitlike. Underleaf bases conspicuously cordate.

This variety (? microspecies) of the *L. elobata–fugax–novae-zelandiae* "complex" appears to be most closely allied to typical *L. novae-zelandiae.* It shares with this the basic leaf form (both taxa tend to have both leaf bases a little cordate); the thick-walled leaf cells, with the marginal cells with the free walls prominently thickened; and the variability in form of the first branch underleaf. In typical *L. novae-zelandiae,* it may be 1-, 2-, 3-, or 4-lobed; in var. *heterostipa,* we have seen only 1-, 2-, or 3-lobed first branch underleaves (Fig. 25 : 8, 9).

In var. *novae-zelandiae,* leaves average rather deeper lobed than in var. *heterostipa:* the wide open ventral sinus usually decends well over 0.5 the leaf length (in var. *heterostipa* the disc, as a whole, is higher and the ventral sinus descends ca. 0.5 the leaf length). The two ventral lobes in typical *L. novae-zelandiae* are separated by a rath-

er broadly V-shaped sinus (in var. *heterostipa* the ventral sinus is often slitlike, and in fact, both dorsal and ventral sinuses may be slitlike or narrowly V-shaped). The bifid leaf associated with a terminal branch in var. *novae-zelandiae* is divided for 0.35–0.45 its length (in var. *heterostipa* it is 0.25–0.3(0.35) bifid; in var. *novae-zelandiae* the disc, to the dorsal sinus, is ca. 6–10 cells high, 8–10 cells high in var. *heterostipa.* Leaf-lobe apices in var. *novae-zelandiae* are more drawn out, with the terminal cells mostly elongated and ca. 2:1 (in var. *heterostipa* lobes are less attenuated and terminal cells are usually under 2:1 [Fig. 25 : 3–5]).

The asymmetry of the leaf in var. *heterostipa* is often relatively slight (Fig. 25 : 1, 10, 11), and the ventral lobes may approach the dorsal ones in length and form. As in typical *L. novae-zelandiae,* well-developed plants have strongly cordate dorsal leaf bases and may have ventral bases dilated and subcordate (Fig. 25 : 10, 11). Underleaves on mature shoots have cordate-auriculate bases.

The variation in lobe number of first branch underleaves is not size related. Thus in Figure 25 : 8, four sectors of a single main stem are shown, each with a branch base; the basal underleaves range successively from 1 to 2 to 1 to 3. The same variation occurs on another shoot (Fig. 25 : 9). Thus the apparently consistent reduction of basal branch underleaves to the monocrural condition in *L. acantha* and *L. elobata* appears to have a genetic basis.

Lepidozia novae-zelandiae var. ***minima*** Schust., var. nov.

Var. novae-zelandiae similis, sed lobis foliaribus et trans latitudinem per 2–3 cellulas et trans longitudinem per 4–6 cellulas extensis, amphigastrio rami primi 1- vel 2-lobo, amphigastriis disco altitudinem per 2 cellulas extenso instructis, lobis plerumque pauci-cellularibus et basi latitudine per 2 cellulas extensis differt.

TYPE—New Zealand, South Is., Fiordland, Falls Creek, *Schuster 48802b.*

Plants rather rigid and wiry, appearing small-leaved (for the stem diameter), the shoots with leaves to ca. 0.7 mm broad. Branching remotely 1-pinnate, the branches short, at right angles to stem, remote; first basal branch underleaf 1- or 2-lobed. Stem rigid, only ca. 6 cells in vertical diameter, with lateral merophytes 4–5 cells broad, ventral merophytes 4 cells broad (underleaves inserted on 4 cell rows); cortical cells rather tangentially flattened, very thick-walled; medulla of rigid, strongly thick-walled cells. Leaves only 175–200 μm broad, asymmetrically 4-fid, the median sinus descending ca. 0.55–0.6, deeper than the dorsal sinus (dorsal pair of lobes forming a perceptible, ± parallel-sided pair); disc ca. 4 cells high to dorsal sinus; dorsal lobes only 2–3 cells broad at base, to 4–6(7) cells long, ending in 2(3) single cells which are 1.5–2 × as long as broad. Underleaves small, the disc usually 2 cells high, the lobes 2(3) cells broad at base, (3)4 cells long.

Figure 26 : 4–13 illustrates this very small, rigid plant. The stem is formed of only 12–13 cortical cell rows (Fig. 26 : 13) and, for a plant of subg. *Notholepidozia,* is formed of a minimal number of cell rows; the rigid, firm-walled medulla is only 4–5 cells high.

Differing from var. *novae-zelandiae* in the 1–2-lobed basal branch underleaves (Fig. 26 : 1, 8), the fewer-celled lobes of leaves (Fig. 26 : 5, 12) and underleaves (Fig. 26 : 4), the much lower leaf disc (Fig. 26 : 5, 12), and underleaves (Fig. 26 : 4). In this plant, the underleaf bases are only ca. 8 cells broad and inserted on 4 rows of cortical cells (Fig. 26 : 4), whereas in var. *novae-zelandiae* underleaf bases are to 10–12 cells broad and inserted on 4–6 rows of cortical cells (Fig. 24 : 14). Although leaf and underleaf margins in var. *minima* are somewhat sinuous, owing to the generally somewhat dilated septa separating marginal cells (Fig. 26 : 5, 12) the marginal cells do not, or only exceptionally, exhibit the constrictions seen in var. *novae-zelandiae* (compare Fig. 26 : 4, 5).

Variety *minima* may be confused with *L. acantha* because of the often unlobed basal branch underleaves (Fig. 26 : 8), but that species has more lanceolate, long-tapered leaf and underleaf lobes formed of many more cells (Fig. 27 : 7); has deeply bifid stem half-leaves associated with branches (Fig. 27 : 5); and has a much more complex stem anatomy, with ca. 22–24 rows of only weakly firm-walled cortical cells (Fig. 27 : 2).

Lepidozia acantha Engel, sp. nov. Figure 27

Amphigastrium primarium ramalinum regulariter non lobatum, subulatum; folia dimidia caulina bifida plerumque 0.45–0.55 longitudinis folii; folia ramulina plerumque 3-loba. Folia quadrifida, 0.5–0.6 longitudinis folii; lobi lanceolati; sinus dorsalis usque 0.5 longitudinis folii descendens; lobi in cellulas elongatas desinentes; cellulae loborum maximam partem rectangulatae.

HOLOTYPE—New Zealand, North Is., Whakarewarewa Thermal Reserve, Sept. 1939, *Hodgson s. n.* (F); isotype: (CHR).

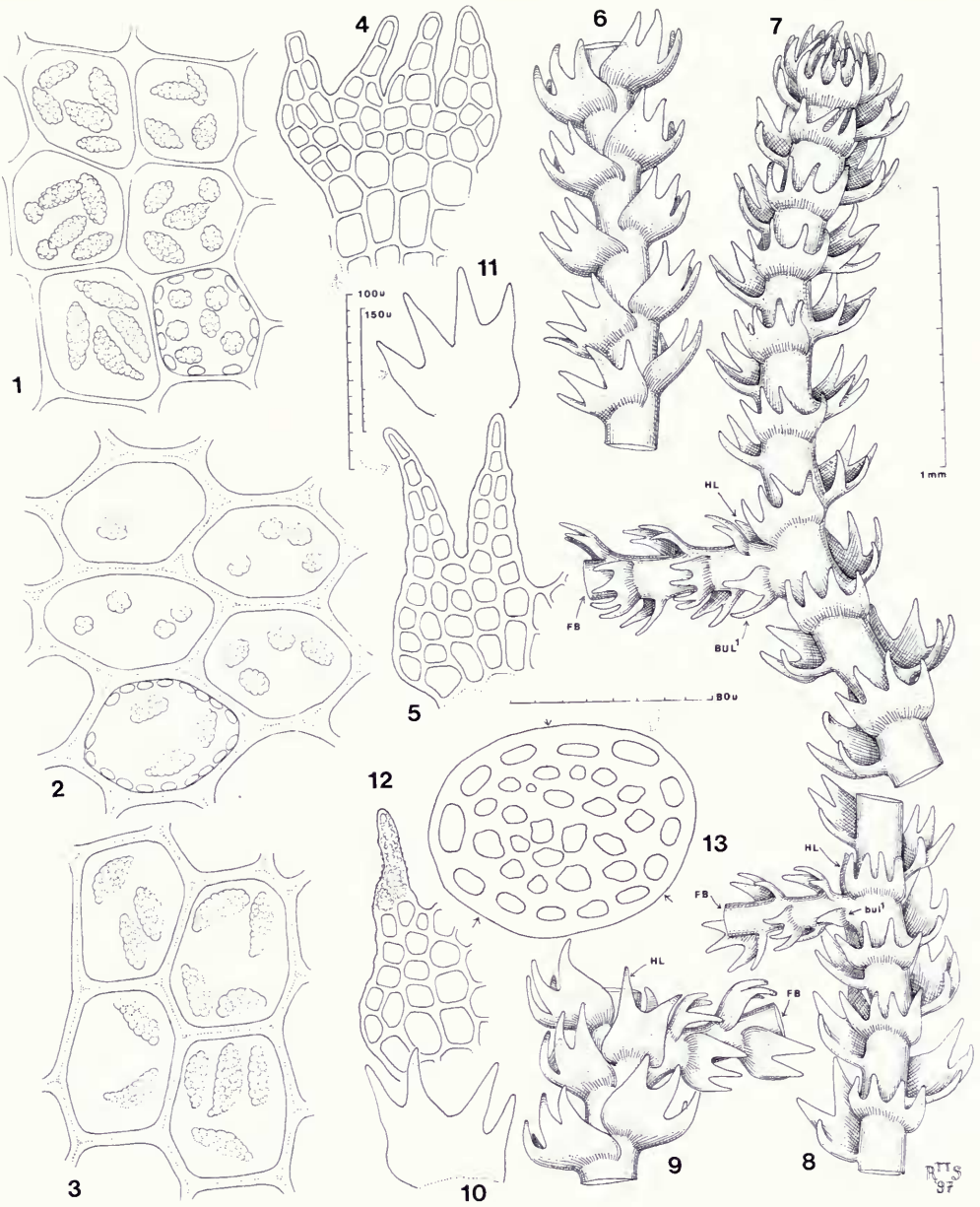

FIG. 26. *Lepidozia* subg. *Lepidozia*; species and subgeneric criteria. (1–3) *Lepidozia spp.,* showing the clearly if finely botryoideal oil-bodies. (4–13) *Lepidozia novae-zelandiae* var. *minima* Schust. **1.** Laminar cells with oil-bodies and, lower right, chloroplasts; oil-bodies 5 × 5–7 to 5 × 10–15 up to 6 × 10–17 μm, 4–6 per cell (×600). **2.** Laminar cells with oil-bodies and, below, chloroplasts; oil-bodies 4–5 to 4.5–5 × 6 to 5 × 7.5–9 up to 5 × 15 to 6 × 11 μm, (1–2) 3–4 (5–6) per cell (×675). **3.** Laminar cells with oil-bodies; oil-bodies 4.5 × 8 to 5 × 11–14 to 5.5 × 9–10 μm, (2)3–5(6) per cell (×725). **4.** Stem underleaf and ventral cortical cells; note size difference and 4 cell-broad merophyte (×235; 100 μm scale). **5.** Dorsal half of leaf (×235; 100 μm scale). **6.** Shoot sector, dorsal aspect (×57.5; 1 mm scale). **7.** Same, ventral aspect; note bifid first branch underleaf, BUL^1, at base of *Frullania*-type branch, FB; at HL, part of dorsal half-leaf visible (×57.5; 1 mm scale). **8.** Same, but with basal branch underleaf (bul^1) unlobed (×57.5; 1 mm scale). **9.** Shoot sector, dorsal aspect, the *Frullania*-type branch (FB) with stem half-leaf (HL) at its base (×57.5; 1 mm scale). **10, 11.** Stem leaves (×110; 150 μm scale). **12.** Dorsal fourth of leaf, distal cells with cuticular papillae drawn in (×235; 100 μm scale). **13.** Stem cross section; at arrows, merophyte margins (×337; 80 μm scale). (Fig. 1 from *Schuster 74-128,* New Zealand, Fiordland, Mt. Burns; 2 from *Schuster 84-146,* New Zealand, Fiordland, Mt. Burns; 3 from *Schuster 84-1027,* New Zealand, Westland, Pakahi; 4–13 from *Schuster 48802b,* New Zealand, Fiordland, Falls Cr.)

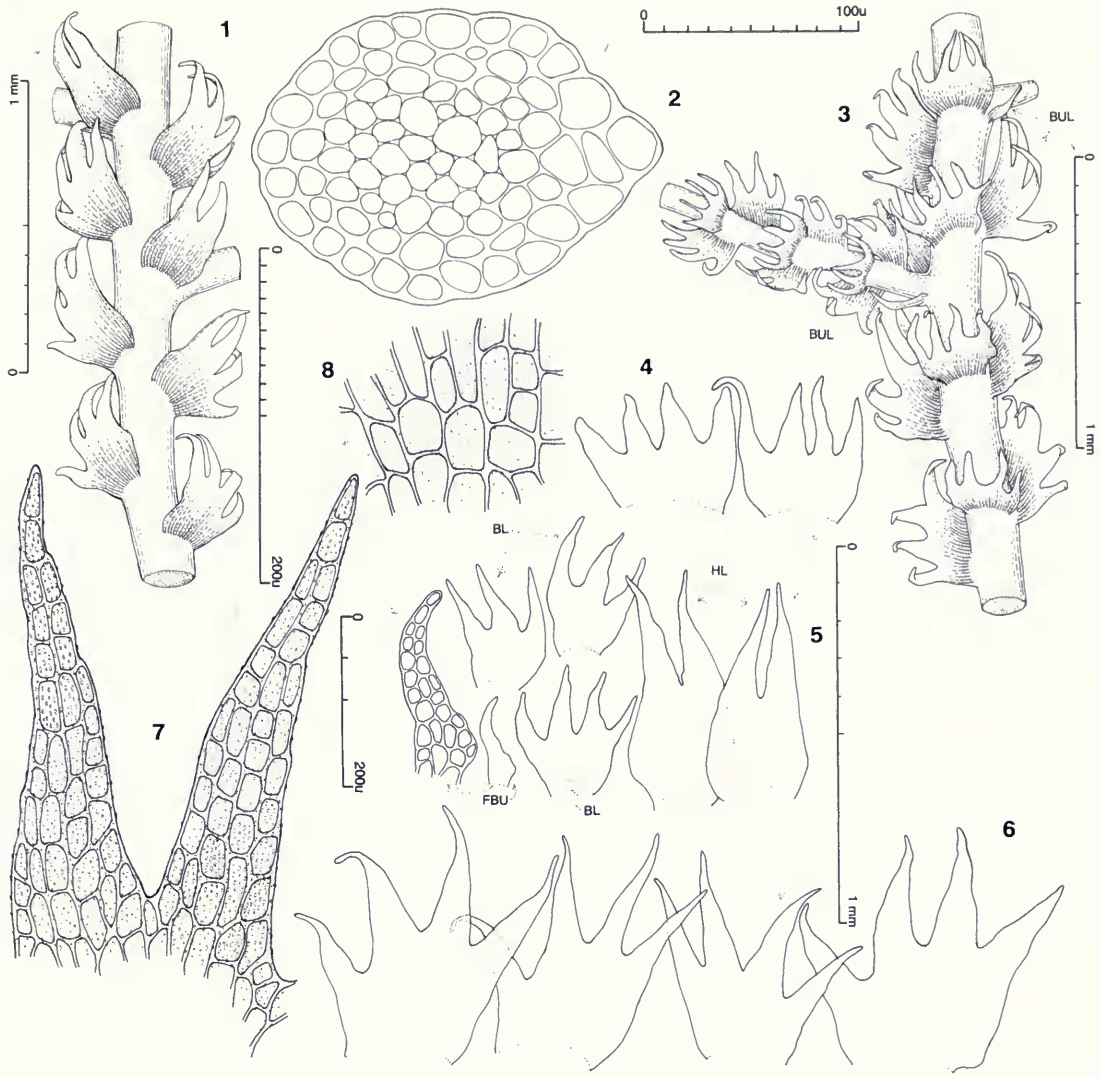

FIG. 27. *Lepidozia acantha* Engel. **1.** Sector of main shoot, dorsal view. **2.** Stem, cross section. **3.** Sector of main shoot with *Frullania*-type branch, ventral view (BUL = first branch underleaf). **4.** Underleaves. **5.** Half-leaves (HL), 3- and 4-lobed primary branch leaves (BL), and, at left, first branch underleaf (FBU) (cellular detail of first branch underleaf at far left). **6.** Leaves. **7.** Leaf lobes (cuticular detail indicated). **8.** Median leaf cells (cuticular detail indicated). (All from type.)

Plants procumbent, in thin mats, slender, flexuous, with spreading branches, pale green, nitid, delicately spinescent when dry, the shoots small to medium, to 1 cm wide (stem to branch extremities). Branching nearly exclusively of *Frullania* type, somewhat irregularly and loosely pinnate, the branches slender, short to elongated and distinctly whiplike, long flagelliform and microphyllous, the nonmicrophyllous leaves deeply subsymmetrically 3–4-lobed; secondary branches not seen; branch half-leaf symmetric, linear, bilobed to 0.5; first branch underleaf undivided and subulate, rarely bilobed, inserted on ventral or ventral-lateral face of main axis and aligned with branch underleaves. Ventral-intercalary branches sporadic, leafy. Stems slender, flexuous. Leaves when dry strongly ventrally secund, with the lobes straight to slightly incurved; leaves when moist strongly spreading, plane or (when lobes slightly incurved) slightly concave, contiguous to distant, with much of stem exposed in dorsal aspect, 0.45–0.65 mm long at longest point × 0.5–

0.65 mm wide at widest point, the insertion distinctly incubous; leaves ± symmetrical, deeply and subequally 4-lobed, divided to ca. 0.5–0.6 (median sinus), the distance from dorsal sinus base to insertion slightly greater than that from ventral sinus to insertion. Lobes long and narrowly attenuate, subequally divergent, the dorsal lobe 5–7 cells wide at the base, the ventral lobes similar to the dorsal in size, the lobes entire, terminating in a single cell or more commonly in a uniseriate row of 2–4 cells; cells of uniseriate row somewhat elongated (up to 2.5 : 1), evenly thick-walled; cuticle of lobes closely and distinctly short striate–papillose. Disc subsymmetrical, subdeltoid, 8–10 cells high at dorsal sinus, 5–8 cells high at ventral sinus, the margins entire, the dorsal margin straight (at most feebly ampliate), the ventral straight, not much shorter than the dorsal. Cells of disc middle moderately and evenly thick-walled, subquadrate to somewhat longitudinally elongated (particularly those aligned with 2nd lobe), 18–23 μm wide × 27–41 μm long; median basal cells larger, in one to several rows; cuticle of disc closely striate papillose, becoming long striate at disc base. Underleaves inserted on 5–7 rows of stem cells, rather large for plant size, ca. 1–1.5 × stem width, plane, spreading, symmetrically quadrifid to ca. 0.5–0.6, the lobes long and slenderly attenuate, ending in a single cell or more often a uniseriate row of 2–3 cells, the cells of uniseriate row quadrate to elongated; disc 4–6 cells high at median sinus; disc margins entire.

Androecia and gynoecia unknown.

DIFFERENTIATION—Resembling *L. bidens* in the narrowly attenuate lobes, the elongation of uniseriate row cells, and the feebly ampliate dorsal margin. It differs in the distinctly incubous leaf insertion (Fig. 27 : 1), the deeply and subequally lobed leaves (Fig. 27 : 6), the closely papillose cuticle (Fig. 27 : 7, 8), the larger underleaves with slenderly attenuate lobes, and the smaller size.

The species has the leaf shape and symmetry of *L. spinosissima* but is a much smaller, procumbent plant, lacking the bipinnate branching, the strongly ventrally secund primary branches, and the transverse leaf insertion of that species.

The disc cuticle is closely striate-papillose (Fig. 27 : 8), as in *L. laevifolia* and its var. *acutiloba*. *Lepidozia acantha* differs from the latter in the narrowly attenuate leaf lobes and from the former in the ± symmetrical leaves, the lobes subequally spreading, and the ventral lobes not widely divergent from the paired dorsal lobes. Suboptimal populations of *L. laevifolia* may key here; see comments under that species.

The species differs from all other New Zealand members of *Lepidozia* except *L. elobata* by the consistently undivided first branch underleaves (Fig. 27 : 3, 5). The name is an allusion to these structures, which resemble miniature "thorns" at the base of each branch. The first branch underleaf is subulate in *L. acantha,* versus rather broad-based and strongly tapered in *L. elobata.* The distinction of these two species is dealt with under *L. elobata.* In *L. elobata,* the half-leaf is only 0.2–0.25 bifid versus 0.4–0.45 in *L. acantha;* leaf lobes are much less tapered, and their end cells are scarcely elongated. It is notable that undivided first branch underleaves are also found in many *Telaranea* species, as is the presence of 3-lobed branch leaves (Fig. 27 : 5); *L. acantha* can be distinguished from superficially similar diminutive *Telaranea* species by the absence of a hyaloderm (Fig. 27 : 2) and the papillose cuticle of the leaves.

DISTRIBUTION–ECOLOGY—Known only from a limited number of New Zealand collections. Found at a single station on South Island at 990 m in Westland Province. North Island populations are from the Rotorua area, at 185 m under manuka and from edges of shaded paths in thermal spring areas, and at ca. 30 m on a very rotted, decorticated, bryophyte-covered log in a mixed broadleaf–podocarp lowland forest (Pakiri Scenic Reserve).

SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. WESTLAND PROV.: Camp Creek, W of Alexander Range, 990 m, *Reif C260A* (F). NORTH ISLAND. SOUTH AUCKLAND PROV.: Rotorua, hot springs area, *Hatcher 34* (F); Waimangu, Rotorua, *Child 412* (F). NORTH AUCKLAND PROV.: Pakiri Scenic Reserve, SSE of Mangawhai Heads, ca. 30 m, *Engel 20300* (F).

Lepidozia elobata Schust., sp. nov. Figure 28

Amphigastrium primarium ramulinum regulariter non lobatum, ovato-lanceolatum; folia dimidia caulina bifida sub 0.25 longitudinis folii attingens; folia ramulina 4-loba. Folia quadrifida, sub 0.5 longitudinis folii attingentia; lobi triangulares, sub lente 3 × longitudine latitudinem aequante; sinus dorsalis plerumque usque 0.2–0.3 longitudinis folii; lobi in cellulas non elongatas desinentes; cellulae loborum maximam partem subquadratae.

HOLOTYPE—New Zealand, North Is., Auckland Harbor, Rangitoto Is., summit area, at tree base, *Schuster 95-401* (F).

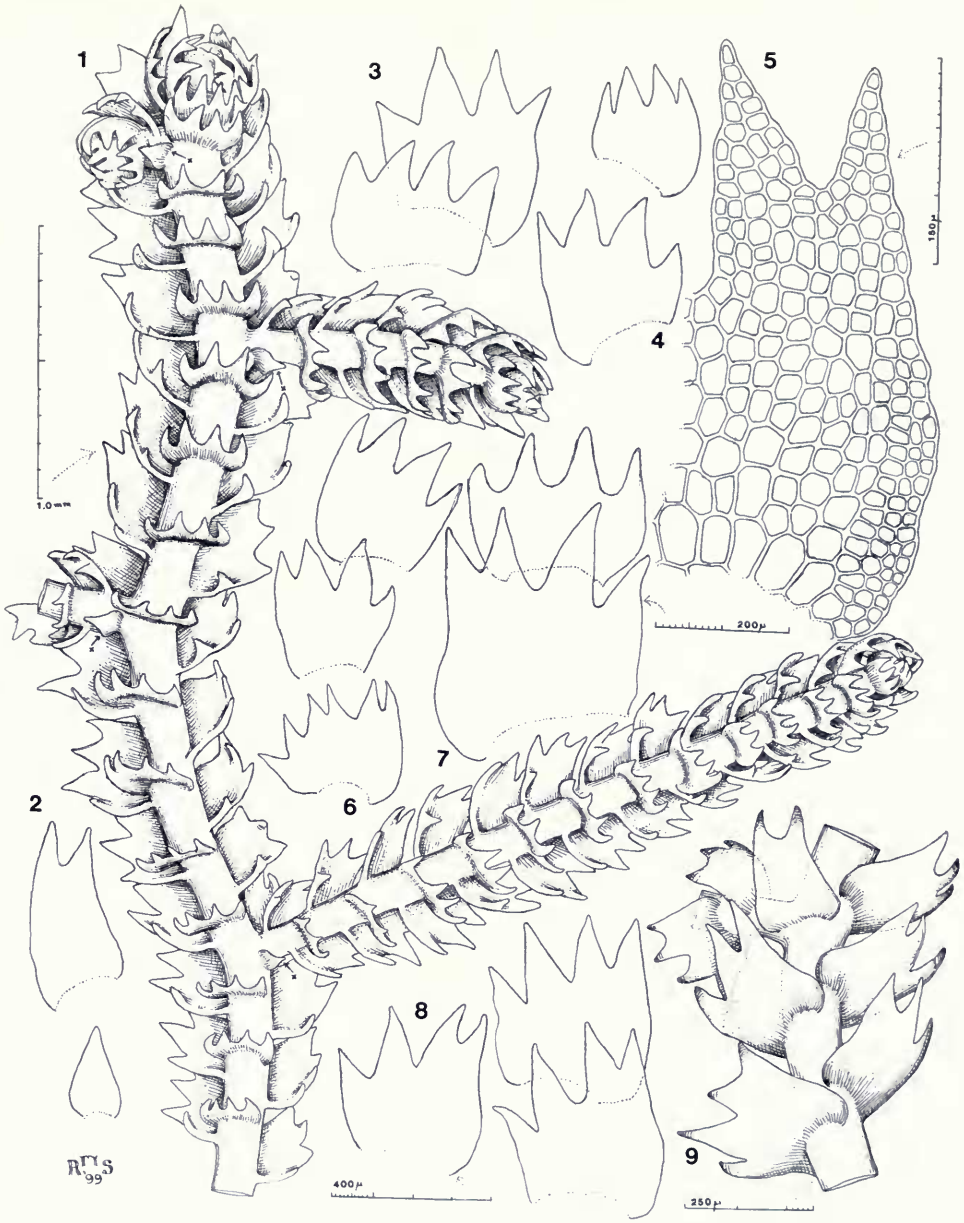

FIG. 28. *Lepidozia elobata* Schust. **1.** Apex of plant, ventral aspect, with three *Frullania*-type branches; at arrows, unlobed basal branch underleaves (HUL[1]) (×36; 1 mm scale). **2.** Stem half-leaf, at branch base (×54; 400 μm scale). **3, 4.** Leaves (×54; 400 μm scale). **5.** Dorsal half of leaf (leaf at arrow, Fig. 8) (×170; 150 μm scale). **6.** Three leaves (×68; 250 μm scale). **7.** Leaf + underleaf (×90; 200 μm scale). **8.** Three leaves (×54; 400 μm scale). **9.** Part of main shoot, dorsal aspect, with *Frullania*-type branch; at HL, stem half-leaf (×68; 250 μm scale). (All from type.)

Plants creeping, light green, whitish when dry, only feebly nitid when dry, small, the main shoots with leaves ca. 430–640 to 700 μm broad; shoot apices and branch apices decurved, especially in drying. Branches almost exclusively of *Frullania* type, 1-pinnate, rather irregularly and remotely so, the branches usually of limited length, but sporadic branches elongating and becoming flagelliform; branch leaves normally similar to stem leaves, quadrilobed like them; first branch underleaf inserted in-line with succeeding branch underleaves, consistently unlobed, ovate lanceolate

to narrowly ovate, ending in a single cell, 80–85 × 130–140 μm (flattened), usually standing stiffly away from stem. Ventral-intercalary branches sporadic, flagelliform. Stems with hyaloderm well-developed, the cortical cells rather thin-walled, oblong (on ventral merophytes ca. 20–22 μm broad × 25–56 μm long). Leaves adaxially concave, the dorsal lobes decurved or deflexed, the ventralmost lobe usually strongly incurved; leaves of leading stems variable, typically quadrilobed for ca. 0.2–0.25(0.3) dorsally to 0.4–0.45 ventrally, the dorsal lobes usually somewhat smaller than the ventral, the lobes acute but never longly acute, ending in 1 or 2 superposed cells that are not or weakly elongated; some to many leaves almost symetrically quadrifid, the lobes then subequal but the two outer lobes usually somewhat smaller; leaf at dorsal base at most weakly cordate. Cells in lobes subquadrate, averaging ca. 11–14 × 13–16 μm, in leaf middle scarcely larger, grading toward base to oblong and 15–18 × 22–27 μm; cells of leaf base much larger, rather inflated, 21–30 × 27–50 μm, forming a small basal field; cuticle weakly papillose above, weakly striolate basally. Underleaves inserted on ca. 5 rows of stem cells, standing stiffly away from stem or subsquarrose, under 0.45 quadrifid, the lobes usually 2 cells broad basally.

No asexual reproduction (leaf lobe apices not caducous). Otherwise unknown.

Differentiation and Variation—Similar to *L. acantha* in (1) the basal branch underleaf is always unlobed; (2) leaves do not consistently show a clear division between a pair of dorsal lobes, set off from the ventral lobes. At times the leaf tends to be almost equally quadrifid, although as in all *Lepidozia* species, the disk is lower ventrally than dorsally.

Lepidozia elobata shows very considerable malleability, often on one shoot, in form and lobing of the leaves. The dorsal pair of lobes is typically separated by a shallower sinus than the sinus separating it from the ventral pair (Fig. 28 : 8), but in *L. acantha,* these two sinuses are usually subequal (Fig. 27 : 6). *Lepidozia elobata* sporadically develops 5- or even 6-lobed leaves (Fig. 28 : 6). On vigorous main stems the three dorsal lobes are often subequal in size and length and only the ventral lobe, which is typically somewhat incurved, is appreciably smaller. However, even the ventral lobe may be rather large, and the leaf may then be subequally quadrifid. Figures 28 : 3, 4, 6–8 shows only part of the variation seen.

In leaf form, especially form of the lobes and depth of sinuses, *L. elobata* approaches *L. pumila.* That species, however, has rather consistently more asymmetrical leaves; the dorsal pair of lobes is consistently much longer than the ventral pair (compare Fig. 29 : 5). By contrast, *Lepidozia pumila* has first branch underleaves consistently 2–4-fid.

Distinct from *L. acantha* in the relatively broad-based, ovate-lanceolate first branch underleaf; the shorter and broader leaf bases, not long-tapered as in *L. acantha;* the subisodiametric cells of leaf-lobe apices; the obscurely papillose cuticle; and the relatively high disk, about as high as or higher than the length of the leaf lobes. In *L. acantha,* branch leaves are typically trifid; in *L. elobata,* they are almost uniformly quadrifid, like the main axis leaves. We have checked branching on several scores of plants: the *Frullania*-type branches uniformly have an unlobed first branch underleaf, and this is ovate or ovate-lanceolate, relatively short and usually rather broad-based compared with that of *L. acantha.*

The first branch underleaf exhibits limited variation. Usually it is broadly lanceolate (Fig. 28 :1, 2), but at times it is unusually small and only 2–3 cells broad at the base; the apex is often uniseriate for 2–3 cells. On weaker shoots, the underleaf is only 2 cells broad for 2–3(4) cell tiers and ends in 2 or 3 single cells. The largest underleaves are 4(5) cells broad basally and contracted to an apex formed of 2(3) superposed cells.

Underleaves in *L. elobata* are uniformly strongly patent, often at right angles to the ventral stem surface; they typically are seen almost edge-on when unflattened plants are examined ventrally. The flattened underleaf is ca. 0.4 quadrifid vs. ca. 0.5–0.6 quadrifid in *L. acantha.* Similarly, the sinuses on stem leaves (and stem half-leaves) are uniformly much shallower in *L. elobata* (cf. Fig. 28 : 2–4, 7, 8, *L. elobata;* compare Fig. 27 : 5, 6, *L. acantha*).

Lepidozia elobata is part of a complex of small species that includes *L. pumila, L. acantha, L. novae-zelandiae,* and *L. bidens.* It can be separated from all taxa of that complex except *L. acantha* by the consistently unlobed first branch underleaves.

Lepidozia pumila Engel, sp. nov. Figure 29

Plantae minutae vel breves, 365–490 μm latae; discus folii ad sinum dorsalem altitudine per 10–12 cellulas extensus e cellulis quadratis vel parum longioribus quam

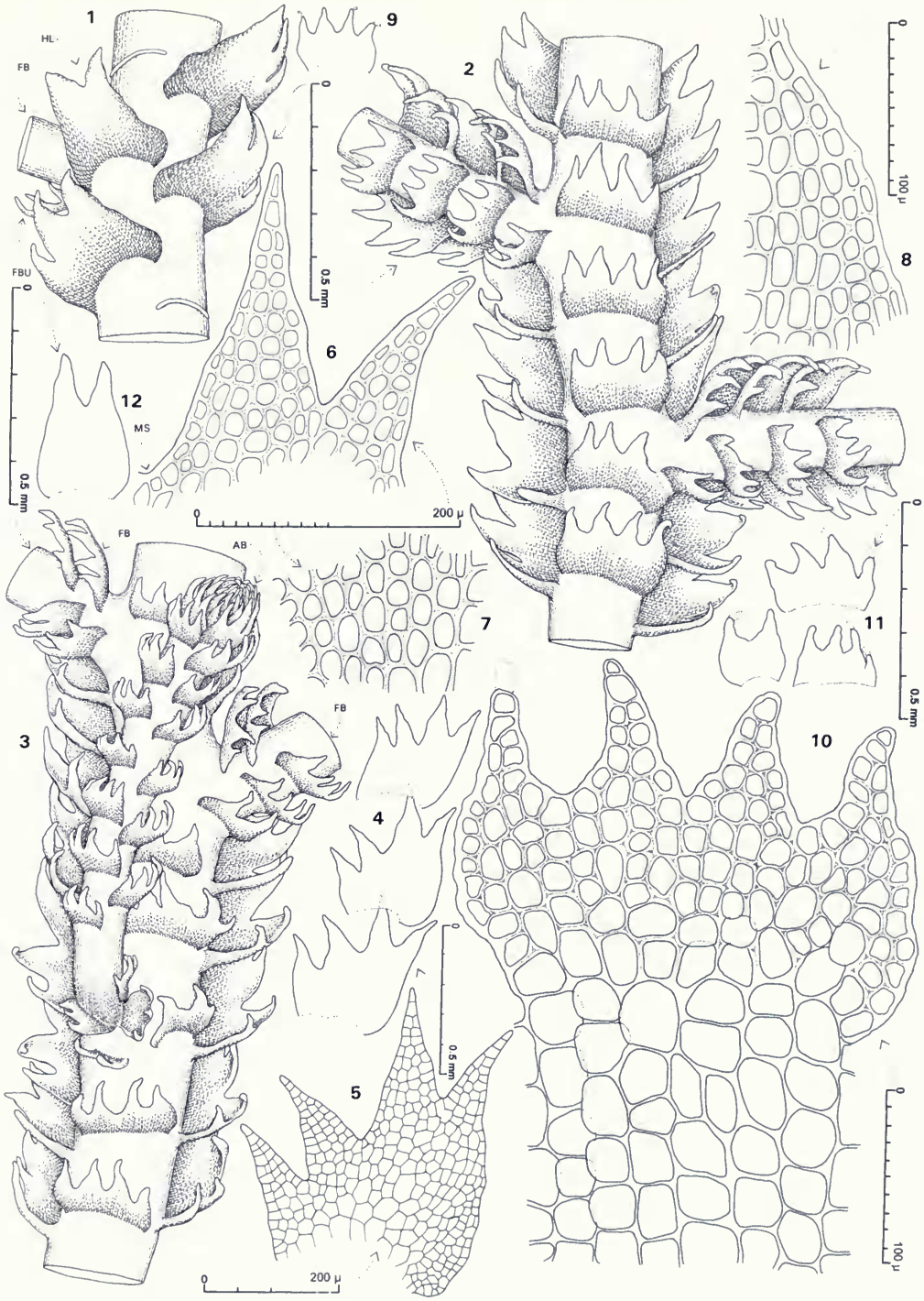

FIG. 29. *Lepidozia pumila* Engel. **1.** Portion of main shoot with *Frullania*-type branch (= FB; HL = half-leaf; FBU = first branch underleaf), dorsal view. **2.** Portion of main shoot with 2 *Frullania*-type branches, ventral view. **3.** Portion of main shoot with *Acromastigum*- (= AB; note half underleaf) and *Frullania*-type (= FB) branches, ventral view. **4.** Three leaves. **5.** Leaf, cellular detail. **6.** Dorsal pair of leaf lobes (ms = median sinus). **7.** Median disc cells. **8.** Marginal cells of dorsal margin of disc showing thickened free wall. **9.** Underleaf (at same scale as Fig. 4). **10.** Portion of stem with underleaf; note ventral merophyte width of 6 cells. **11.** First branch underleaves. **12.** Half-leaf. (All from type.)

latioribus compositus; lobi dorsales cellulis series uniseriatae subisodiametris vel parum longioribus quam latioribus instructi; cutis cellularis disci foliaris laeva; cellulae lobi laeves vel non distincte papillosae; amphigastria in 5–6 seriebus cellularum caulinarum inserta.

HOLOTYPE—New Zealand, South Is., Fiordland Natl. Park, Moraine Creek, Hollyford Valley, ca. 400-650 ft., *Schuster 48111a* (F); isotype: (CHR).

Plants closely prostrate, flexuous, with spreading branches, green, nitid when dry, the shoots minute to small, 365–490 μm wide (leaf tip to leaf tip), plant to 5 mm wide, including branches. Branching nearly exclusively of *Frullania* type, rather short, usually irregularly and distantly pinnate to ± regularly pinnate, the primary (and secondary) branches often becoming whiplike, flagelliform, and microphyllous, the nonmicrophyllous leaves ± symmetrically 4-lobed; primary branches often developing into new leading shoots; secondary branches occasional, 1–4 per primary branch; branch half-leaf subsymmetrical, cordate, 2-lobed to ca. 0.3; first branch underleaf (1)2–4-lobed, inserted on ventral side of branch base to the ventral-lateral side of junction of main axis and branch, in both cases the first branch underleaf aligned with underleaves of branch. *Acromastigum*-type branches (?) occasional. Ventral-intercalary branching occasional, leafy. Stems flexuous. Leaves cup-shaped (with the tips of the lobes incurved and not visible in dorsal view) to concave, contiguous, with much of stem visible in dorsal view, somewhat longer than wide, (0.25)0.4–0.5 mm long and wide, spreading, the insertion weakly to distinctly incubous; leaves usually strongly asymmetrical, 4(5)-lobed, the leaves divided to ca. 0.45–0.55 (median sinus), the distance from dorsal sinus base to insertion much greater than that from ventral sinus to insertion. Lobes attenuate, somewhat apiculate, the dorsal lobes sometimes paired, the two ventral shorter and somewhat divergent from the dorsal lobes, the lobes entire, terminating in a uniseriate row of 2–4 cells, the cells of uniseriate row ± isodiametric or slightly longer than wide, thick-walled; dorsal lobe (2)3–5 cells wide at base; cuticle of lobes smooth or faintly and indistinctly papillose. Disc asymmetrical, obliquely truncate and deltoid, 10–12 cells high at dorsal sinus, 4–6 cells high at ventral sinus, the margins entire, the dorsal margin ± straight, abruptly cordate near the base, the ventral margin shorter than the dorsal, at times distinctly so. Cells of disc middle evenly and distinctly thick-walled, occasionally with small trigones, 20–33 μm wide and long; median basal cells in 1 (locally 2) rows of enlarged cells; marginal cells of disc and lobes with a thickened outer wall; cuticle of disc smooth. Underleaves inserted on 5–6 rows of stem cells, spreading, short, broader than high, symmetrically 4-fid to ca. 0.4–0.55 (median sinus), the lobes plane, slenderly acuminate, often only 2–3 cells wide at base, entire, terminating in a uniseriate row of 3–5 cells; disc 4–5(6) cells high at median sinus, the margins plane, entire.

Plants dioecious. Androecia not seen. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; gynoecium base bulbous, fleshy, polystratose and rhizoidous; bracts of innermost series much larger than leaves, erect and sheathing the perianth, the bracts deeply concave, broadly ovate; apices 2–4-dentate-lobulate, each lobule terminating in a single cell or a uniseriate row of 2 cells, the cells of lobule base may have a cell on each side that projects at its distal end to form a crenulation, the lobules otherwise composed of subrectangular to subsinuate cells; lamina composed of ± regularly subrectangular cells, the margin bordered by thin- to slightly thick-walled cells of variable shape and orientation, some hardly longer than wide, others ± sinuate-rhomboidal, the apical or free end of marginal cells slightly divergent and forming a short projection, the margin irregularly and often sparingly crenulate, the margin otherwise entire except for a sporadic single-celled tooth; bracteole similar in size and form. Perianth rather long and prominent, slenderly cylindrical-fusiform, straight, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth, the lobes composed of ± tiered, narrowly subrectangular cells, the distalmost tier with cells that at the apical end are laterally free for varying lengths, the lobes crenate-subdenticulate; perianth cells ± regularly subrectangular below mouth, and here the cuticle is finely striate; perianth 2–4 stratose near base.

Seta with 8 rows of outer cells surrounding an inner core of numerous much smaller cells. Capsule oblong, the wall 38–41 μm thick, of 3 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheetlike thickenings and several large nodulelike to spinelike thickenings alternating with those that are devoid of thickenings (or, rarely, are locally thickened), the transverse walls usually devoid of thickenings or sporadically with an isolated nod-

ule; semiannular bands sporadic; innermost layer of cells ± tiered, narrowly rectangular, semiannular bands common, close and numerous, sometimes incomplete, not forked.

Spores 13.9–14.9 μm, exine brown, with dense, rather coarse but low, sharply defined papillae and simple or furcate vermiculate markings. Elaters rigid, nontortuous, 7.7–9.6 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 3.4–3.8 μm wide.

DIFFERENTIATION—This smallest New Zealand member of the *laevifolia* group is evidently rather rare. Suboptimal expressions of *L. laevifolia* with poorly developed cuticular papillae may well be mistaken for this species. For further details, see the discussion under *L. laevifolia.*

A minute phenotype of the species occurs in median and upper elevations on cliff faces and boulders and forms pure, tight, compact mats of usually wirelike, upright shoots. Examples are *Engel 17564* from a cliff face at 670 m on Mt. Cargill (Otago Prov.), and *Engel 18668* from a subalpine boulder at 1010 m in the Mt. Burns area (Southland Prov.). Shoots are ca. 350–400 μm (not including branches), and leaves are minute (400–500 μm wide and long) and in dry plants quite inconspicuous. Despite their seemingly impoverished condition, these specimens bear mature perianths.

Lepidozia pumila and *L. bidens* are closely related in many respects: they share similar leaf shapes, with the dorsal pair of lobes much longer than the ventral (compare Figs. 29 : 4, 5 and 30 : 2, 3); both have median-basal disc cells relatively large versus distal and peripheral cells (Figs. 29 : 5; 30 : 3); both have leaf lobes acute, ending in 2–3 superposed cells. The former, however, is a minute to small species (the smallest member of sect. *Notholepidozia*), yet has a leaf disc 10–13 cells high at the dorsal sinus, while the latter is a medium-sized plant but has a leaf disc 8–10 cells high at the dorsal sinus. Also, *L. pumila* has underleaves inserted on 5–6 rows of stem cells (Fig. 29 : 10), whereas *L. bidens* has underleaves inserted on 8 rows of stem cells (Fig. 30 : 10). The species are for the most part separated ecologically: *L. pumila* typically occurs from 570 m into the subalpine zone, whereas *L. bidens* is strictly a forest species (on South Island only at low elevations).

This species and *L. spinosissima* are the only members of the genus *Lepidozia* known to have ventral-terminal branching (Fig. 29 : 3). Branches of this type are diagnostic for the genus *Acromastigum* but otherwise occur only sporadically in the family—in, for example, *Kurzia mollis, Neogrollea,* and *Paracromastigum.* Taxa with this branch type typically are erect (*K. mollis*) or, occasionally, loosely prostrate (*Acromastigum cavifolium* Schust.), but are not closely prostrate as in *L. pumila.*

DISTRIBUTION–ECOLOGY—Auckland Is., New Zealand (North Is., South Is.). A species occurring over a broad elevational gradient. It occurs in forests ranging from 570 m to the upper reaches of the forest and found corticolous or on shaded, moist, cliff faces and boulders. It ranges up to 1370 m in the subalpine zone on rock (particularly with some soil accumulation) or in rock crevices. Occasionally (type) in lower elevation forests (120–200 m) over wet humus of the shaded forest floor, and then occurring with *L. pendulina.*

SELECTED SPECIMENS SEEN—AUCKLAND IS.: 1 mile W of Trinity Cove, Carnley Harbour, *Johnson 19/8* (WELT). NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Fiordland Natl. Park, valley just SW of Mt. Burns, S of South Branch of Borland Burn, W of Monowai, 1010–1170 m, *Engel 18668* (F); Garvie Range, East Dome, ca. 1370 m, *Child H 3892* (F). OTAGO PROV.: S side of Mt. Cargill, just below summit, N of Dunedin, ca. 670 m, *Engel 17564* (F); Kakanui Range, ca. 1525 m, *Child H 2827* (F); Mt. Aspiring Natl. Park, ridge below and W of Mt. Shrimpton, 1250 m, *Engel 17857* (F). OTAGO/WESTLAND PROV. BOUNDARY: Summit area of Haast Pass, 570 m, *Engel 18003* (F). WESTLAND PROV.: Arthur's Pass Natl. Park, Lower Otira Bridge, *Engel 6799* (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Arthur's Pass, near Temple Basin Ski area, *Engel 6449A* (F). CANTERBURY PROV.: Mt. Cook Natl. Park, Governors Bush, SW of town of Mt. Cook, 760–800 m, *Engel 18193* (F); Arthur's Pass Natl. Park, immediately below Punchbowl Falls, *Engel 6900* (F); summit of Mt. Tourlesse, *Hatcher 1214* (F). MARLBOROUGH PROV.: Branch River, ca. 305 m, *Child H 4367* (F). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, Taranaki Falls Track, E of Whakapapa Village, 1080 m, *Engel 22441* (F). TARANAKI PROV.: Pukeiti Bush, near New Plymouth, *Hatcher 261* (F). GISBORNE PROV.: Lake Waikaremoana, *Hatcher 1308* (F).

Lepidozia bidens Engel, sp. nov. Figure 30

Plantae regulariter pinnatae, amplitudine medianae, 700–900 μm latae; folia lobis dorsalibus distincte binatis instructa, anguste attenuata, in seriem uniseriatam e cellulis elongatis (usque 2:1) compositam terminantia; discus foliaris ad sinum dorsalem altitudine per 8–10 cellulas extensus e cellulis plus minusve longitudinaliter

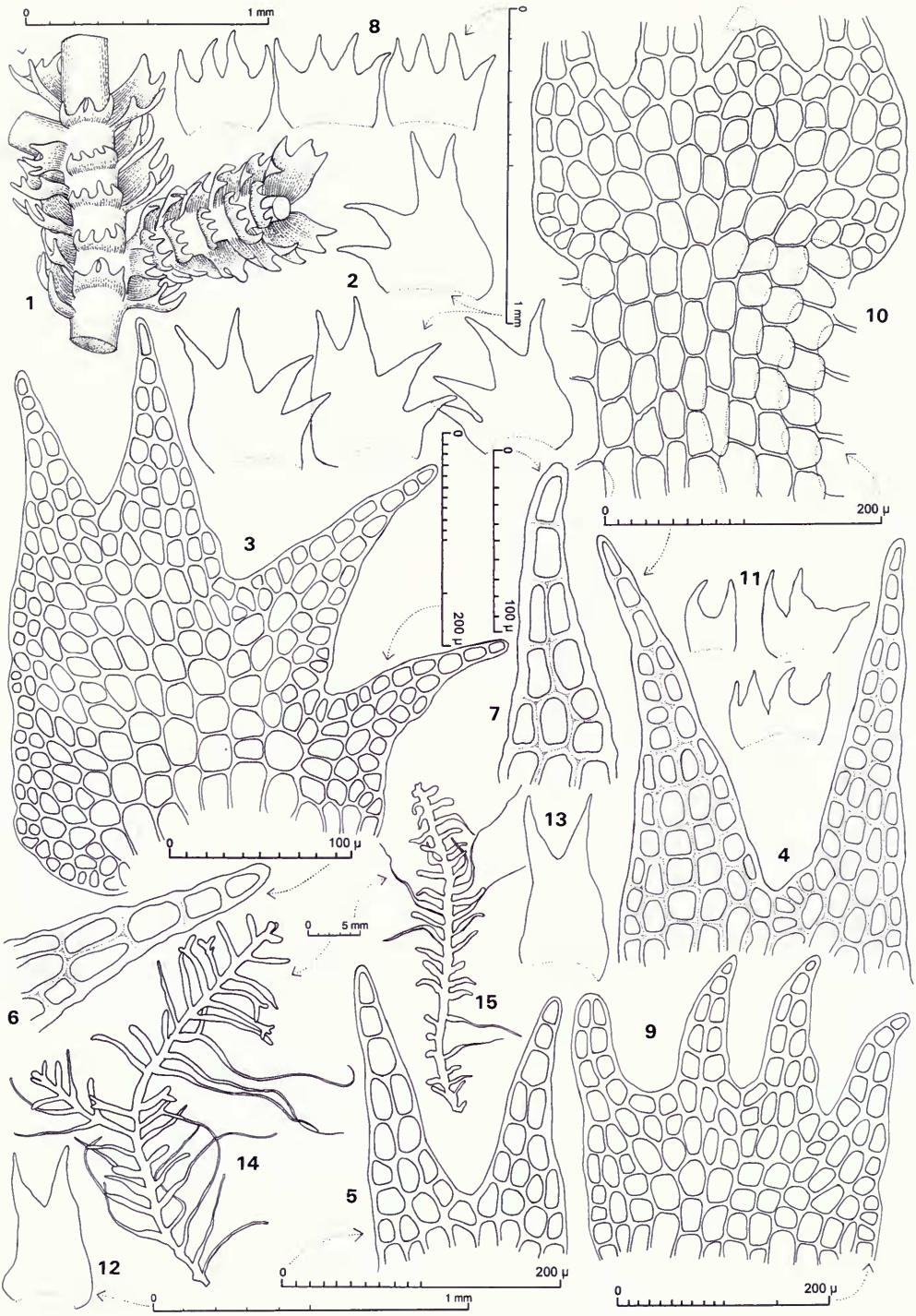

FIG. 30. *Lepidozia bidens* Engel. **1.** Sector of main shoot with *Frullania*-type branch, ventral view. **2.** Leaves. **3.** Leaf. **4, 5.** Dorsal pairs of leaf lobes. **6, 7.** Dorsal lobes. **8.** Underleaves. **9.** Underleaf. **10.** Portion of stem with underleaf; note ventral merophyte width of 8 cells. **11.** Two-, 3- and 4-lobed first branch underleaves (drawn to same scale as Fig. 8). **12, 13.** Half-leaves (3). **14, 15.** Outlines of two shoots at low magnification. (Figs. 1 from *Engel 19280,* New Zealand, Nelson Prov., Paparoa Range, N side of Tiropahi or Four Mile River; 2, 3, 5–11, 15 from type; 4, 12–14 from *Child 358,* New Zealand, South Is., Westland Prov., Fox Glacier.)

elongatis compositus; amphigastria in seriebus octo cellularum caulinarum inserta.

HOLOTYPE—New Zealand, South Is., Nelson/Westland Prov. boundary, Paparoa Range, S side of Porarari River, up river from gorge and ca. 500 m WSW of ford on inland track to Bullock Creek, 10–20 m, *Engel 19204*—c. per. (F); isotype: (CHR).

Plants procumbent, in thin mats, slender, flexuous, with spreading branches, pale green, nitid, delicately spinescent when dry, the shoots small to medium, to 1.5 cm wide (stem to branch extremities). Branching exclusively of *Frullania* type, regularly pinnate, the branches slender, short to greatly elongated and distinctly whiplike, long-flagelliform, microphyllous, the nonmicrophyllous leaves subsymmetrically 4-lobed, the primary branches occasionally developing into new leading shoots; secondary branches sporadic to occasional, 1(2) per primary branch; branch half-leaf symmetrical, linear (at times slightly broadening toward base), 2 (rarely 3)-lobed to 0.3–0.45; first branch underleaf (2)3–4-lobed, inserted on ventral side of branch base or at juncture of branch and main axis, aligned with branch underleaves. Ventral-intercalary branches not seen. Stems slender, flexuous. Leaves when dry slightly concave, with tips of lobes straight to slightly and broadly incurved; leaves when moist spreading, slightly concave, contiguous to distant, with much of stem exposed in dorsal aspect, 0.45–0.5 mm long × 0.35–0.5 mm wide, the insertion subtransverse to weakly incubous; leaves distinctly asymmetrical, unequally 4(5)-lobed, divided to ca. 0.5–0.65 (median sinus), the distance from dorsal sinus base to insertion much greater than that from ventral sinus to insertion. Lobes long and narrowly attenuate (the dorsal lobes especially so), the dorsal lobes parallel to somewhat divergent (rarely approaching 90°), ± distinctly paired, 3–5 cells wide at base, the ventral lobes often shorter, curved and spreading (often at right angles to the dorsal margin), the lobes entire, terminating in a uniseriate row of 2–3 cells; cells of lobes and uniseriate row somewhat elongated (up to 2:1, but the terminal 1–2 cells sometimes subquadrate), evenly thick-walled; cuticle of lobes smooth to faintly striate-papillose. Disc strongly asymmetrical, subdeltoid, 8–10 cells high at dorsal sinus, 4–5 cells high at ventral sinus, the margins entire, the dorsal margin straight (at most feebly ampliate), the ventral straight, much shorter than the dorsal. Cells of disc middle moderately and evenly thick-walled, ± longitudinally elongated, particularly those in the dorsal half of leaf, 18–31 μm wide × 30–50 μm long; median basal cells distinctly larger, in 1 to several rows; marginal cells of disc and lobes with a thickened outer wall; cuticle of disc smooth to faintly striate-papillose. Underleaves inserted on 8 rows of stem cells, small, ca. 1–1.1 × stem width, plane, strongly spreading to squarrose, symmetrically quadrifid to ca. 0.4–0.5, the lobes attenuate, ending in a single cell or a uniseriate row of 2–3 cells, the cells of uniseriate row often elongated; disc 4–6 cells high at median sinus; disc margins entire.

Plants dioecious. Androecia not seen. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series much larger than leaves, erect and sheathing the perianth, the bracts deeply concave, narrowly ovate to suborbicular; apices with 2–4 short, irregular lobes composed of ± regularly rectangular + irregularly and feebly sinuate-rhomboidal cells, the apical end of the marginal cells often feebly to distinctly diverging, the lobes crenate-denticulate to spinose dentate; lamina composed of ± regularly short-rectangular cells, the margin bordered by cells of variable shape, some long and narrow, others hardly longer than wide, the apical or free end of marginal cells variously divergent and forming a short projection or a tooth, the margin irregularly crenate-denticulate to the base, the teeth at times composed of a few to several cells; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth, the lobes composed of feebly tiered, long, narrow, subrectangular to sinuate-rhomboidal, thick-walled cells; mouth cells thick-walled, especially at the summit, at the apical end laterally free for varying lengths, the mouth thus crenate-denticulate; perianth cells ± regularly rather short subrectangular below mouth, and here the cuticle is long striate; perianth 2-stratose near base.

Sporophyte not seen.

DIFFERENTIATION—The species may be immediately distinguished by the distinctly paired, long, narrowly attenuate, dorsal lobes, which lend a delicately spinescent appearance to dried plants (Fig. 30 : 3–5). Related to this feature is the distinctive appearance of the half-leaves, which are

linear and deeply divided (up to 0.5; Fig. 30 : 12, 13). The ventral lobes are typically shorter than the dorsal, curved and spreading, often at nearly right angles to the dorsal margin (Fig. 30 : 2, 3). The species also has distinctive areolation; median cells of the disc are often elongated, particularly in the dorsal half of the leaf, and the median basal cells are larger in contrast to those along the dorsal and ventral margins (Fig. 30 : 3).

Lepidozia bidens belongs to a complex of small to minute species that includes *L. novae-zelandiae, L. acantha,* and *L. laevifolia*; however, *L. bidens* differs from the other three in its regularly pinnate branching (Fig. 30 : 14, 15) and generally larger size.

Distribution–Ecology—A forest plant of both South and North Islands. On South Island it occurs in wet, rich, lower-elevation forests (sea level to 330 m) in banks of bryophytes, or it may be corticolous (on, for example, *Fuchsia*). It also may occur in open forests (again, below 330 m) of, for example, *Nothofagus fusca* and *Dacrydium cupressinum,* and here it occurs in large masses at tree bases. On North Island it occurs, for example, on rotted, decorticated, bryophyte-covered logs in the mature podocarp forest at Whirinaki Forest Park. The species reaches higher elevations on North Island, occurring at 920 m on bryophyte-covered wood in the beach–remu–totara forests at Waikareiti Track (Urewera Natl. Park), and (also Urewera Natl. Park), at 720 m, on the sides of old *Sphagnum* mounds in a low, open, boggy area with *Sphagnum* hummocks, *Leptospermum scoparium,* and *Dracophyllum subulatum* at Waipai Swamp.

Selected Specimens Seen—NEW ZEALAND. SOUTH ISLAND. OTAGO PROV.: Morrisons Creek, N of Dunedin, 330 m, *Engel 17709* (F). WESTLAND PROV.: Cascade Road, Cascade ultramafic moraine, W of Martyr Saddle, SSW of Jackson Bay, ca. 35 m, *Engel 21775* (F); Fox Glacier, sea level, *Child 358* (F); Westland Natl. Park, Lake Wombat, 250 m, *Engel 6671* (F). NELSON PROV.: Paparoa Range, N side of Tiropahi or Four Mile River, W side of Route 6 ca. 500 m N of bridge over river, 145 m, *Engel 19280* (F). NORTH ISLAND: WELLINGTON PROV.: Tree Trunk Gorge, W bank of Tongariro River, E border of Tongariro Natl. Park, boundry of Kaimanawa State Forest Park, ca. 700 m, *Engel 21191* (F). GISBORNE PROV.: Urewera Natl. Park, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 650–920 m, *Engel 20586* (F); ibid., Waipai Swamp, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 720 m, *Engel 20601* (F). TARANAKI PROV.: Pukeiti Bush near New Plymouth, *Hatcher 410* (F). SOUTH AUCKLAND PROV.: Whirinaki Forest Park, Waterfall Loop track, near Whirinaki River, SSW of Minginui, *Engel 20689* (F).

Sect. *Kirkii* Schust.

Lepidozia sect. *Kirkii* Schust., Beih. Nova Hedwigia 118: 197. 2000.

Plants primarily 1-pinnate, but longer branches sometimes with 1–2(3) secondary branches; *Frullania*-type branches with basal branch underleaf normally trifid, often with a few marginal teeth, oriented "in line" with succeeding underleaves and clearly on ventral side of plant. Leaves imbricate, clearly incubous, asymmetrical, with ampliate dorsal margin, relatively shallowly and subequally quadrilobed (ventral sinus clearly deeper, descending 0.35–0.5 leaf length), the dorsal margin of disc (usually) and dorsal 1–2 lobes (sparingly), rather remotely, coarsely and variably toothed.

Type—*Lepidozia kirkii* Steph.

Including *L. kirkii* and *L. hirta.* The two species are clearly similar in most respects, including the coarse, often oblique dentition of the dorsal leaf margins and the large lacinium on each side of the underleaf, so that underleaves appear 6-lobed. Distinctive for the group is the position of the initial branch underleaf; this is aligned with succeeding branch underleaves (Fig. 31 : 3, 4), and the underleaf is very similar in form to succeeding branch underleaves, differing chiefly in being trilobed.

Lepidozia kirkii Steph. Figure 31

Lepidozia kirkii Steph., Spec. Hep. 3: 598. 1909. Original material: New Zealand, South and North Is., *Krone, Beckett, Kirk* (*non vidi*).
Lepidozia dentifolia Steph., Spec. Hep. 3: 599. 1909, *syn. nov.* Original material: New Zealand, Jacksons Track, *Goebel* (G!).

Plants ascending, rather flexuous, with ventrally secund branches, pale green, the shoots medium, to 2 cm wide, including branches. Branching mostly of *Frullania* type, regularly pinnate, the primary branches often becoming whiplike, flagelliform, microphyllous, and rooting in the substrate, the primary branches often developing into new leading shoots; secondary branches occasionally present, 1–3 per primary branch, often arising in distal half of primary branch, the secondary branches normally not longer than the primary; branch half-leaf ± symmetrical to slightly asymmetrical, broadly ovate, shallowly 2(3)-lobed to 0.3, irregularly toothed nearly to the base; first

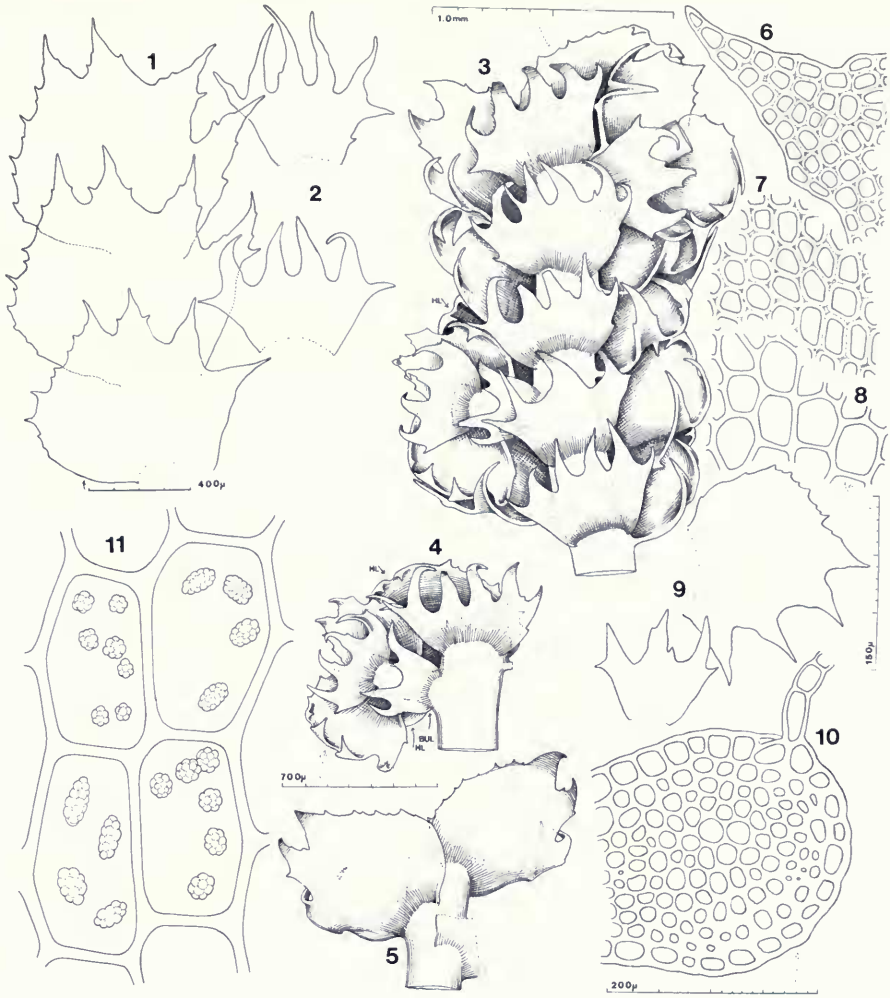

FIG. 31. *Lepidozia kirkii* Steph. **1, 2.** Three stem leaves and two underleaves (×32; 400 μm scale). **3.** Shoot sector, ventral aspect, with two *Frullania*-type branches; at HL, the dorsal half stem leaf (×32; 1 mm scale). **4.** Shoot sector, ventral aspect; the dorsal half stem leaf (HL) visible; at BUL, the first branch underleaf, which is already in the "normal" position vis à vis the branch (×30; 700 μm scale). **5.** Shoot sector, dorsal aspect (×30; 700 μm scale). **6, 8.** Cells of lobe apex, middle, and base (×153; 150 μm scale). **9.** Stem leaf and adjacent first branch underleaf (×30; 700 μm scale). **10.** Stem cross section (×140; 200 μm scale). **11.** Cells of lobe middle (× ca. 780). (All from *Schuster 67-254,* New Zealand, South Is., Westland, Omeroa River.)

branch underleaf 4(5)-lobed, inserted on ventral to ventral-lateral (side facing shoot base) side of branch and aligned with underleaves of branch. Ventral-intercalary branching rare and sporadic, leafy. Stems soft, flexuous, 10–12 cells in diameter, the cortical cells in 1 layer of thick-walled cells somewhat larger than the medullary cells; medullary cells thick-walled, rather uniform in size. Leaves rigid, concave, with incurved lobes, imbricate and completely hiding stem in dorsal view, 0.6–0.95 mm long at longest point, 0.8–1.4 mm wide at widest point, patent, the insertion distinctly incubous and slightly recurved at dorsal end; leaves distinctly asymmetrical, unequally 4-lobed, the leaves divided to ca. 0.4–0.55 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion. Lobes of differing shape, the dorsal pair of lobes acute, the ventral lobe narrowly acuminate to sublinear, the lobes ± divergent, the dorsal pair of lobes partially united, the lobes entire or sometimes with 1 to several short teeth, the dorsal lobe 9–14 cells wide at base, the lobes terminating in a single cell or a uniseriate row of 2–3 cells

(the ventral often somewhat longer); cells of uniseriate row ± isodiametric to slightly longer than wide, thick-walled. Disc distinctly asymmetrical, 22–27(30) cells high at dorsal sinus, 10–14 cells high at ventral sinus; dorsal margin broadly ampliate, the dorsal margin and the confluent margin of dorsal lobe irregularly (often doubly) dentate or serrate (erose) by teeth of 1 to several cells (the margin at times with a few weak teeth); ventral margin much shorter than the dorsal, entire or sometimes with a process. Cells of disc middle evenly thick-walled, ± isodiametric to longitudinally elongate, 14–22 × 18–30(36) μm; median basal cells enlarged, in 1–2 rows, with irregularly thickened walls; cuticle smooth to indistinctly striate-papillose. Underleaves spreading, symmetrically 4-fid to ca. 0.45–0.6 (median sinus), the sinus bases somewhat reflexed, the lobes incurved, ± parallel, gradually attenuate, entire or with a tooth or spine, usually blunt at the tip or terminating in a single cell or short uniseriate row of 2–3(5) cells; disc 10–15 cells high at median sinus, disc margins somewhat reflexed, on each side with a lobelike process distally, the underleaves then appearing 6-lobed.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, cernuous ventral-intercalary branches mostly from main shoot and occasionally from primary branches; bracts ventricose-cucullate, 2-lobed to ca. 0.3–0.4, the lobes acute, the lateral margins entire or with a tooth and a few slime papillae; antheridia 1–2 per bract, the stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series much larger than leaves, erect and sheathing the perianth, the bracts deeply concave, broadly ovate; apices with 4 short, ± regular lobes composed of ± regularly rectangular and (especially at the lobe extremities) irregularly sinuate-rhomboidal cells, the apical end of the marginal cells often diverging and forming a tooth, the lobes thus crenate-denticulate; lamina composed of ± regularly subrectangular cells, the margin bordered by thin-walled cells of variable shape and orientation, some hardly longer than wide, others ± sinuate-rhomboidal, the apical or free end of marginal cells variously divergent and forming a short projection or a tooth, the margin irregularly crenate-denticulate (+ slime papillae) to the base, the teeth at most of 3 superposed cells; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed, somewhat contorted mouth, the lobes composed of irregularly sinuate-rhomboidal cells that at the apical end are laterally free for varying lengths, the lobes crenate-denticulate; perianth cells ± regularly subrectangular below mouth area and here the cuticle is conspicuously striate; perianth 2–3 stratose near base.

Seta with 10–14 rows of outer cells surrounding an inner core of numerous much smaller cells. Capsule elliptical to oblong, the wall 52–54 μm thick, of (4)5 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheetlike thickenings and several large nodules alternating with walls that are devoid of thickenings (or are sporadically locally thickened), the transverse walls usually devoid of thickenings or sporadically have an isolated nodule; innermost layer of cells with ± tiered, narrowly rectangular, semiannular bands common, close and numerous, sometimes incomplete, rarely forked.

Spores 14.4–15.8 μm, exine brown, with coarse, high, sharply defined, widely spaced papillae and simple or furcate vermiculate markings that sometimes coalesce (but do not delimit areolae). Elaters rigid, nontortuous, 9.6–11.5 μm wide, only slightly tapering toward tips, bispiral, the spirals 3.4–3.8 μm wide.

DIFFERENTIATION—The dorsal margin of the leaf disc and the confluent margin of the dorsal lobe are typically coarsely and irregularly (often doubly) dentate or serrate (Fig. 31 : 1), rather than armed with discrete spines (terminating in a uniseriate row of 2 or more cells), as in *L. hirta* (Fig. 32 : 2, 4, 10). Presence of teeth, even when few in number, will distinguish the species. *Lepidozia hirta* also differs in the more deeply lobed underleaves with the lobes often variously and irregularly dissected.

DISTRIBUTION–ECOLOGY—Auckland Is., New Zealand (South Is., North Is.).

The species occurs in forests over a variety of substrates (rock, tree bark, rotten logs) over a broad altitudinal range (ca. 30–1230 m). It is present in the upper limits of *Nothofagus menziesii* forests as well as in forests dominated by *Nothofagus solandri* var. *cliffortioides*. It also extends to the upper reaches of the subalpine zone (1040–1110 m), where it forms tufts on rock. In forested sites it occurs with *Goebeliella, Lepicolea scolopendra, Lepidolaena taylori, Bazzania adnexa,*

and others. In the southern sectors of South Island, it occurs at 100 m or lower; for example, the species occurs over soil of vertical, bryophyte-covered banks in *Nothofagus truncata* forests (90 m in Nelson Prov., *Engel 21545*) to the mataitotara flood plain forests (110 m in Westland Prov., *Engel 18923*), where it is corticolous. On North Island it is may be found in open forests dominated by *Weinmannia racemosa, Kunzea ericoides,* and *Agathis australis,* and it occurs over bare rock of cliff faces (820 m in South Auckland Prov., *Engel 22409*).

SELECTED SPECIMENS SEEN—AUCKLAND IS.: Head of North Arm, Carnley Harbour, 15 m, *Johnson 22/8* (welt). NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Fiordland Natl. Park, off track to Island Lake, just W of Borland Saddle, S of South Branch of Borland Burn, W of Monowai, 800 m, *Engel 18642* (F); ibid., near Lake Thompson Hut, on track to George Sound, W of Lake Te Anau, ca. 290 m, *Schuster 48297c* as *L. ulothrix* (F). OTAGO PROV.: Fiordland Natl. Park, head of Lake McKerrow, near McKerrow Hut, *Hatcher 1446* (F). Mt. Aspiring Natl. Park, Blue Valley Track, above Blue River just N of confluence with Makaroa River, 430–480 m, *Engel 21920* (F). WESTLAND PROV.: Jackson Bay, between confluence of Jackson River and Arawata River and Lake Ellery, off Jackson River Road, ca. 30 m, *Child H4267* (F); Mt. Aspiring Natl. Park, Cross Creek, 1.1 km N of Haast Pass, 540 m, *Engel 21885* (F); Westland Natl. Park, Franz Josef Glacier Valley, off Roberts Point Track, SW of Mt. Gunn, ca. 510–570 m, *Engel 18136* (F); ibid., along Gillespies Cook River Road, between Tornado Creek and Whelan Creek, *Engel 6604* (F); near Waiho River between Lake Wombat Terrace and Canavans Knob, NW of town of Franz Josef Glacier, off Hwy 6, 110 m, *Engel 18923* (F); Camp Creek, W of Alexander Range, 500–905 m, *Reif C62D, C229F* (F); Arthur's Pass Natl. Park, Kelly Range, off track to Carroll Hut, above Kellys Creek, N of Otira, 1,040–1,110 m, *Engel 18431* (F); Paparoa Range, road to Sewell Peak, 710 m, *Engel 19067* (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Arthur's Pass, near Temple Basin Ski area, *Engel 6495*—c. ♂ (F). NELSON PROV.: Track to German Terrace, 6 km SSE of Westport on Nine Mile Road, 90 m, *Engel 21545* (F). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, Blyth Track, along small stream ca. 0.5 km from Ohakune Mt. Road, ca. 1230 m, *Engel 21306* (F). TARANAKI PROV.: Pukeiti Bush, near New Plymouth, *Hatcher 249* (F). SOUTH AUCKLAND PROV.: Coromandel State Forest Park, ridge just W of summit of Table Mt., 820 m, *Engel 22409* (F).

Lepidozia hirta Steph. Figure 32

Lepidozia hirta Steph., Spec. Hep. 3: 599. 1909. Original material: New Zealand, without specific loc., *Kirk* (G!).

Lepidozia angelii Gott. *ex* Steph., Spec. Hep. 3: 596. 1909. Original material: New Zealand, without specific loc., (*Angel*) (G!).

Plants delicate, loosely procumbent, rather flexuous, soft and plumose, with weakly ventrally secund branches, pale green, the shoots medium, to 1.7 cm wide, including branches. Branching mostly of *Frullania* type, closely and regularly pinnate, primary branches becoming whiplike, flagelliform, microphyllous, and rooting in the substrate; secondary branches rarely present; branch half-leaf ± symmetrical to slightly asymmetrical, broadly ovate, shallowly 2-lobed, ± regularly spinose-dentate nearly to the base; first branch underleaf 4(5) lobed, inserted on ventral to ventral-lateral (side facing shoot base) side of branch and ± aligned with underleaves of branch; second branch underleaf in a strong morphologically ventral position. Ventral-intercalary branching occasional, stoloniform. Stems rather soft, flexuous. Leaves rigid, concave, with incurved lobes, imbricate and nearly or completely hiding stem in dorsal view, 0.4–0.5 mm long at longest point, 0.6–0.8 mm wide at widest point, patent, the insertion distinctly incubous and feebly recurved at dorsal end; leaves distinctly asymmetrical, unequally 4-lobed, the leaves divided to ca. 0.4–0.65 (median sinus), the lobes ± divergent, the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion, the sinuses gradually becoming deeper ventrally. Lobes of differing shape, the dorsal pair of lobes caudate, the ventral lobe attenuate, often spreading as a claw, the dorsal lobes not noticeably paired, the lobes entire or with a single prominent spine or with a few small, often opposing teeth, the dorsal lobes (5)9–11 cells wide at base, terminating in a uniseriate row of 2–3(6) cells (the ventral often somewhat longer); cells of uniseriate row ± isodiametric to somewhat longer than wide (2:1 or less), not noticeably longer than basal cells in lobe, thick-walled. Disc weakly asymmetrical, 10–16 high at dorsal sinus, 5–8 cells high at ventral sinus; dorsal margin broadly curved to subampliate, the dorsal margin and the confluent margin of the dorsal lobe ± regularly spinose-dentate with 3–6 discrete, short, acuminate, often curved, multicellular spines (the margin often also with several few-celled teeth); ventral margin much shorter than the dorsal, entire. Cells of disc middle thick-walled, ± isodiametric to elongate, 12–18 × 18–25 μm; median basal cells enlarged, in 1–2 rows, with trigones and irregularly thickened walls; cuticle striate-papillose. Underleaves

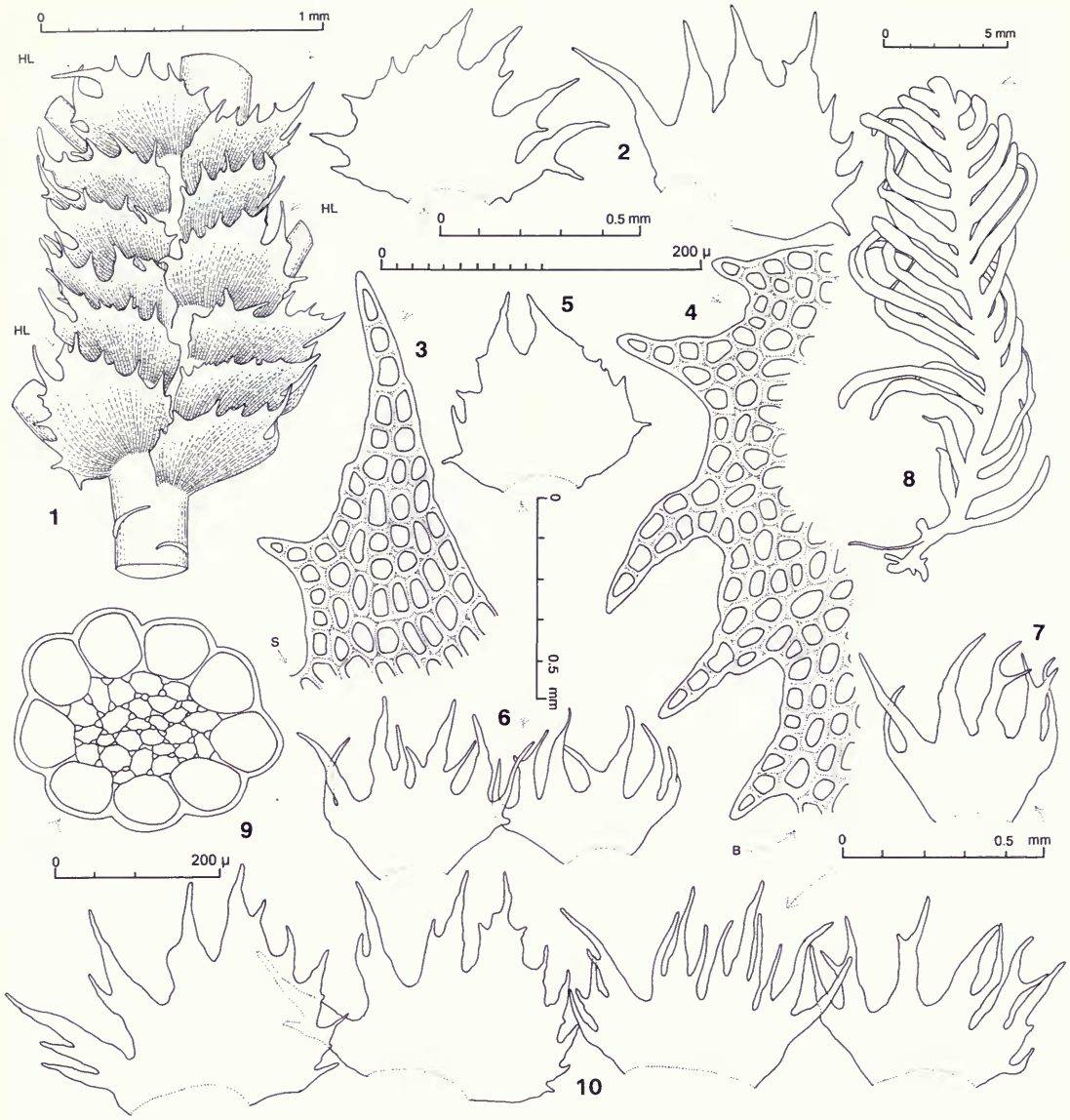

FIG. 32. *Lepidozia hirta* Steph. **1.** Sector of main shoot, dorsal view (hl = half-leaf). **2.** Leaves. **3.** Dorsalmost lobe of leaf (s = sinus). **4.** Dorsal margin of leaf (B = leaf base). **5.** Half-leaf. **6, 7.** Underleaves. **8.** Outline of plant at low magnification. **9.** Seta, cross section. **10.** Two leaves and to right, two underleaves, all at same scale. (Figs. 1–8 from *Engel 19205,* New Zealand, South Is., Nelson/Westland Prov. boundary, Paparoa Range, S side of Porarari River; 9 from *Hatcher 136,* New Zealand, South Is., Canterbury Prov., Mt. Tourlesse; 10 from *Braggins 94/241,* New Zealand, North Auckland Prov., SE corner of Waipoua Forest.)

spreading, symmetrically 4-fid to ca. 0.55–0.8 (median sinus), the sinus bases somewhat reflexed, the lobes broadly incurved, somewhat divergent, narrowly attenuate, variable: entire to variously and irregularly dissected (with one to several lobuliform spines), the lobes terminating in a uniseriate row of 3–6 cells; disc 6–9 cells high at median sinus, disc margins on each side with a lobelike spine, the underleaves then appearing 6-lobed.

Plants dioecious. Androecia not seen. Gynoecia on abbreviated ventral–intercalary branches issuing from main stem; bracts of innermost series much larger than leaves, erect and sheathing the

perianth, the bracts deeply concave to canaliculate, ovate to suboblate; apices with 2–4 teeth or short, irregular lobes or unlobed, the distal cells of bracts as well as cells of teeth and lobes composed of irregularly sinuate-rhomboidal cells that at their apical end are laterally free for varying lengths, the lobes crenate-denticulate; lamina composed of ± regularly subrectangular cells, the margin bordered by thin-walled cells of variable shape and orientation, some hardly longer than wide, others ± sinuate-rhomboidal, the apical or free end of marginal cells variously divergent and forming a short projection or tooth, the margin irregularly and at times sparingly crenate-denticulate to the base, the teeth at most of 2 superposed cells; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly 3-plicate toward mouth, the perianth gradually narrowing toward the distinctly contracted, obscurely ca. 6-lobulate mouth, the lobules composed of irregularly sinuate-rhomboidal, thick-walled cells that at the apical end are laterally free for varying lengths, the lobules thus irregularly crenate-denticulate; perianth cells ± regularly subrectangular below mouth area; perianth 2 stratose near base.

Seta with 9 rows of outer cells surrounding an inner core of numerous much smaller cells. Capsule oblong, the wall 50–53 μm thick, of 4 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheetlike thickenings and several low, broad nodules alternating with walls that are devoid of thickenings, the transverse walls usually devoid of thickenings or sporadically have 1–2 isolated nodules; innermost layer of cells ± tiered, narrowly to rather broadly rectangular, the longitudinal walls with nodular to spinelike thickenings and, often, somewhat sinuous sheetlike thickenings, semiannular bands sporadic, never forked.

Spores 38.4–42 μm, exine yellow-brown, thin, with low, dense, close papillae and short, sometimes branched, vermiculate markings that sometimes coalesce but do not delimit areolae. Elaters rigid, nontortuous, 24–30 μm wide, only slightly tapering toward tips, bispiral, the spirals 9.6–10.8 μm wide.

DIFFERENTIATION—*Lepidozia hirta* differs from *L. ulothrix* in its smaller leaves, its closely and regularly pinnate branching (Fig. 32 : 8), the branches often becoming whiplike and rooting in the substrate. Typically, *L. ulothrix* is a more robust plant, with distant, abbreviated, somewhat curved branches.

For comments distinguishing this species from *L. ulothrix* and *L. kirkii,* see under those species.

Among the traditionally cited synonyms of *L. ulothrix* are two Stephani names that apply to this taxon, *L. hirta* and *L. angelii,* published simultaneously in 1909. The types of both names have been examined and are quite similar; *L. hirta* is considered the more appropriate name.

DISTRIBUTION–ECOLOGY—Endemic to New Zealand (South Is., North Is.). It occurs, for example, at the edges of rills in the subalpine zone in areas with mostly snow tussock, but with some *Dracophyllum longifolium, Celmisia, Empodisma minor,* and others (*Engel 19022*). At the Mangawhero River site (*Engel 21288*), it occurred in low *Nothofagus solandri* var. *cliffortioides* forest with steep, moist, peaty, mossy banks; in the Paeroa Range (*Allison H2995*), it occurred on very old logs in an upper-elevation forest. At the Waipoua Forest site (*Braggins 94/241*), the species occurred over rotted wood in a very wet *Weinmannia silvicola-Syzygium maire* forest.

SELECTED SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. WESTLAND PROV.: Paparoa Range, ridge immediately N of Sewell Peak, 890 m, *Engel 19022* (F). NELSON/WESTLAND PROV. BOUNDARY: Paparoa Range, S side of Porarari River, up river from gorge and ca. 500 m WSW of ford on inland track to Bullock Creek, 10–20 m, *Engel 19205*—c. sporo. (F). CANTERBURY PROV.: Mt. Tourlesse, *Hatcher 136*—c. sporo. (F). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, west-facing steep bank of Mangawhero River, off Ohakune Mt. Road, ca. 1200 m, *Engel 21288* (F). SOUTH AUCKLAND PROV.: Paeroa Range, S of Rotorua, ca. 915 m, *Allison H2995* (F). NORTH AUCKLAND PROV.: SE corner of Waipoua Forest, Mataraurau Plateau, 540 m, *Braggins 94/241* (AKU).

Subg. *Austrolepidozia* Schust.

Lepidozia subg. *Austrolepidozia* Schust., Beih. Nova Hedwigia 118: 197. 2000. Type: *Lepidozia ulothrix* (Schwägr.) Lindenb.

Lepidozia Ill. *Incisae* Lindenb. *in* G. L. & N., Syn. Hep. 210. 1845, *syn. nov.* Lectotype (*nov.*): *Lepidozia ulothrix* (Schwägr.) Lindenb.

Plants normally 1-pinnate, the branches of limited length, sporadically to frequently the lower becoming flagelliform; stem half-leaf ovate, shallowly (to 0.35–0.4) bilobed, lobes with 1–3 cilia, disc copiously spinose-dentate; basal branch underleaf variably (2)3–4-lobed, bearing or ending in 1–2(3) cilia. Stem with hyaloderm relatively

distinct, weakly firm-walled, the medulla relatively uniform, smaller-celled, prominently thick-walled. Leaves asymmetrically ovate, the dorsal margin strongly convex and ampliate, the ventral margin short, straight to concave-sided; dorsal sinus descending ca. 0.4–0.45 leaf length, the disc high dorsally; ventral sinus descending less than 0.65 the leaf length; dorsal margin copiously ciliate-dentate to ciliate, the cilia mostly shorter than those of lobes; ventral margin usually eciliate; dorsal 1–2 lobes mostly with (1)2–3(4) cilia or teeth, mostly alternate, sporadically in 1(2) opposed pairs; ventral 1–2 lobes with mostly only 1–2(3) long cilia, alternate. Cells in disc and cilia thick-walled, rigid, in cilia in large part strongly elongated (2–5: 1); cuticle smooth to obscurely striolate. Underleaves obdeltoid to obtrapezoidal, 0.6–0.7 quadrifid; disc 1-ciliate to edentate; lobes with 1–3 cilia, if 2 often opposed.

Apparently monotypic.

We have debated placing *Austrolepidozia* as a mere section of subg. *Chaetolepidozia* Schust.[12] Both groups bear strongly spinose-ciliate leaves, the cilia formed in large part of prominently elongated, rigid cells. *Chaetolepidozia, s. str.*, is quite different in (1) the very deeply quadrifid leaves in which the dorsal lobe is not strongly ampliate basally; (2) the lobes all freely ciliate, even the ventral with up to 10–12 cilia, often secondarily bifid; (3) cilia, except for the distalmost, usually clearly oriented in opposed pairs; (4) underleaves freely ciliate, each usually with (1)2 pairs of opposed cilia; (5) stem half-leaf at branch bases normally trifid, asymmetrical, the sinuses descending to 0.75–0.8, the lobes with (1)2–3 pairs of opposed cilia; and (6) basal branch underleaves mostly deeply bifid, sporadically one lobe again bifid, with sinuses descending to within 0.2–0.25 of the base, freely ciliate with often opposed pairs of long cilia.

Lepidozia ulothrix (Schwägr.) Lindenb. Figures 33 and 34

Jungermannia ulothrix Schwägr., Hist. Musc. Hep. Prodr. 21. 1814. *Lepidozia ulothrix* (Schwägr.) Lindenb. *in* G. L. & N., Syn. Hep. 210. 1845. *Mastigophora ulothrix* (Schwägr.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. Original material: "N. Hollandia," without specific locality, "Herb. Ldbg," *sin. coll.* (G!).

Jungermannia albula Hook. f. & Tayl., London J. Bot. 3: 387. 1844, *syn. nov. Lepidozia albula* (Hook. f. & Tayl.) G. L. & N., Syn Hep. 211. 1845. *Mastigophora albula* (Hook. f. & Tayl.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. Original material: Auckland Is., "on *Gottschea lehmanniana,*" Nov., 1840, *Hooker* (FH!).

Plants rather delicate, flexuous, with weakly ventrally secund branches, pale olive green to whitish green, the shoots medium-sized, to 2 cm wide, including branches. Branching exclusively of *Frullania* type, distantly markedly and regularly pinnate, the primary branches short, somewhat curved or hooked at the tip, occasionally becoming flagelliform but not extensively so; secondary branches only sporadically present, then 1 per primary branch, the secondary branches not longer than the primary; branch half-leaf asymmetrical to ± symmetrical, ovate, 2-lobed, regularly ciliate nearly to the base; first branch underleaf (2)3–4 lobed, inserted on ventral-lateral (side facing shoot base) side of branch (often at extreme base of branch) and aligned with underleaves of branch; second branch underleaves in a ± strong morphologically ventral position or the 2nd–4th cycles of branch underleaves gradually becoming truly ventral. Ventral-intercalary branching lacking. Stems rather soft and flexuous, 10–13 cells in diameter, the cortical cells in 1 layer of weakly to clearly thick-walled cells (the exposed wall sometimes particularly thickened) that are slightly to conspicuously larger than medullary cells; medullary cells distinctly thick-walled in cross section, often with marked trigonelike thickenings. Leaves rigid, strongly concave, with incurved lobes lending the leaves a ± cuplike aspect, imbricate and nearly or completely hiding stem in dorsal view, 0.4–1.2 mm long at longest point, 0.7–2.2 mm wide at widest point, patent, the insertion distinctly incubous and slightly recurved at dorsal end; leaves distinctly asymmetrical, unequally 4-lobed, the leaves divided to ca. 0.4–0.65 (median sinus), the lobes suberect or only slightly divergent, the distance from dorsal sinus base to insertion much greater than that from ventral sinus to insertion, the dorsal lobes not noticeably paired, the sinuses gradually becoming deeper ventrally. Lobes of differing shape, the dorsal pair of lobes caudate, the ventral lobe linear to attenuate, the lobes with 1 to (less often) several pairs of opposing spines (1[2], non-opposing spines per lobe in suboptimal plants) the dorsal lobes 7–10 to 13–15 cells wide at base, the ventral lobe 6–9 cells wide at base, the lobes ter-

[12] For subg. *Chaetolepidozia,* see Schuster (2000). Piippo (1984) recognized the group as *Lepidozia* at the section level.

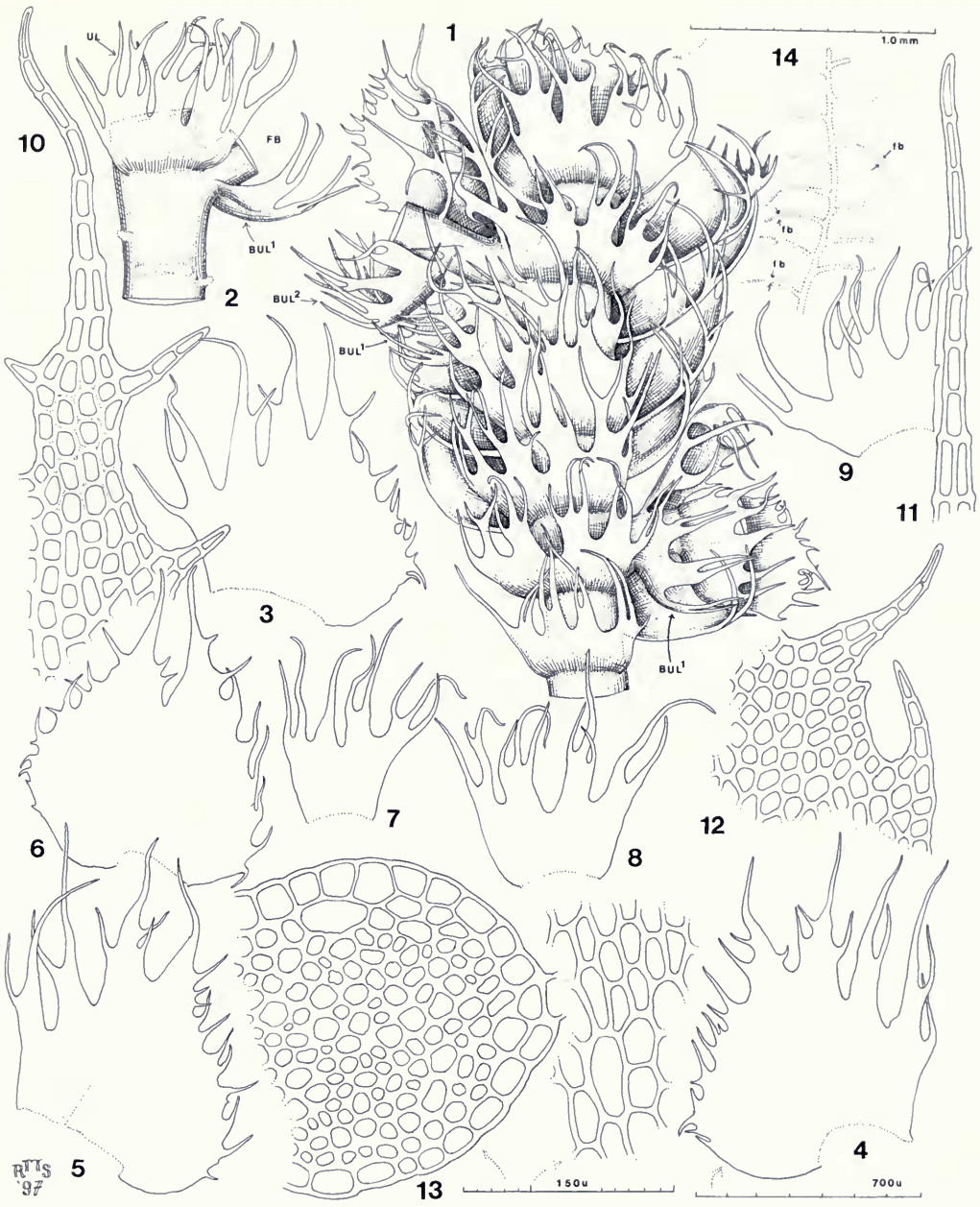

FIG. 33. *Lepidozia ulothrix* (Schwaegr.) Lindenb. **1.** Part of main axis, ventral aspect, with bases of two *Frullania*-type branches; at BUL[1], first branch underleaf; at BUL[2], second branch underleaf (×34; 1 mm scale). **2.** Part of main stem with underleaf; at right base of *Frullania*-type branch (FB) with (BUL[1]) basal branch underleaf; at UL, stem underleaf (×34; 1 mm scale). **3, 5.** Main stem leaves (×45; 700 μm scale). **6.** Stem half-leaf associated with branch (×45; 700 μm scale). **7.** Optimal-sized basal branch underleaf (×45; 700 μm scale). **8, 9.** Stem underleaves (×45; 700 μm scale). **10.** Apex of dorsal leaf lobe (×195; 150 μm scale). **11.** Tip of ventral leaf lobe (×195; 150 μm scale). **12.** Part of dorsal leaf margin (×195; 150 μm scale). **13.** Stem cross section and surface view of cortical cells (×195; 150 μm scale). **14.** Cladograph; double lines = leafy shoot sectors; single lines = flagella; at fb = initiation of flagellar branch (× 1.75). (All from *Schuster 95-1924,* New Zealand.)

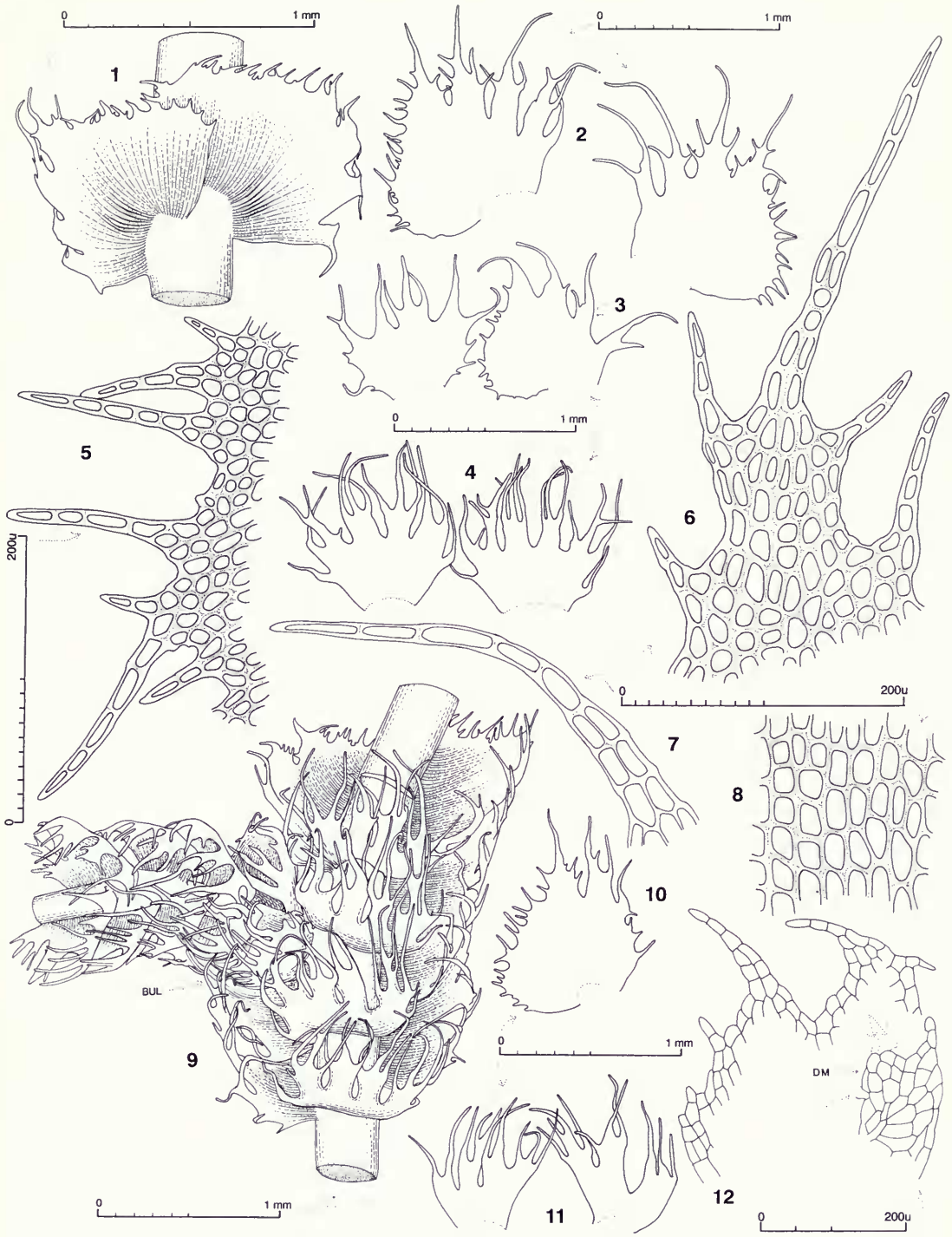

FIG. 34. *Lepidozia ulothrix* (Schwaegr.) Lindenb. **1.** Sector of main shoot, dorsal view. **2.** Leaves. **3.** Underleaf; at right, leaf. **4.** Underleaves. **5.** Sector of dorsal margin of leaf. **6.** Portion of dorsal lobe. **7.** Distal sector of dorsalmost leaf lobe. **8.** Median disc cells of leaf. **9.** Sector of main shoot with *Frullania*-type branch, ventral view (BUL = first branch underleaf). **10.** Half-leaf. **11.** First branch underleaves. **12.** ♂ Bract (DM = dilated dorsal margin, slime papillae at arrows). (Figs. 1, 2, 4–6, 8–11 from *Fife 8987,* New Zealand, South Is., Arthur's Pass Natl. Park, Bealey Glacier Track; 3, 7 from type of *L. albula.*)

minating in a uniseriate row of 5–7 to 8–10(15) cells (the ventral typically the longest); cells of uniseriate row capillary, elongated (3–4:1), thick-walled and with the septa thickened and swollen. Disc distinctly asymmetrical, primarily due to strong dilation of dorsal sector, the dilated portion up to a third of the disc area, the disc 18–26 cells high at dorsal sinus, 6–13 cells high at ventral sinus; dorsal margin and the confluent margin of the dorsal lobe with 7–8 to 12–19 spinose teeth or cilia that terminate in a uniseriate row of 2–5(6) cells; ventral margin much shorter than the dorsal, entire or sporadically with 1–2 well-developed spines or laciniae. Cells of disc middle evenly thick-walled, elongate, 12–20 μm × 24–42 μm; cells in the ampliate sector and median lobe cells shorter, 14–18 μm × (17)20–26 μm; median basal cells enlarged and in a rather distinct field; cuticle smooth to finely striate-papillose. Oil-bodies 2–4 per cell, ovoid or globose, botryoidal, mostly 4–6 μm in greater diam. Underleaves 1.5–2 × stem width, spreading, symmetrically basically 4-fid to ca. 0.45–0.65 (median sinus), the sinus bases plane, the lobes distinctly broadly incurved, the lobe base ± parallel-sided, 8–9 cells wide, the summit of median lobes truncate and ± regularly ciliiform 2–3-fid, the distal sector setaceous, terminating in a uniseriate row of 5–8 to 8–13 cells; disc 10–13 cells high at median sinus, disc margins on each side with 1–2 cilia.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, cernuous ventral-intercalary branches from main shoot and primary and secondary branches (the androecial branches often not exceeding tips of underleaf lobes); bracts ventricose-cucullate, 2-lobed to ca. 0.4, the lobes acuminate, terminating in a uniseriate row of 2–4 elongated cells, the lobe margins with several spinose teeth; dorsal margin of disc slightly dilated in basal sector to form a feebly to moderately rounded projection, the dilated portion with several slime papillae; ventral margin of disc with several spinose teeth or laciniae; antheridia 1 per bract, the stalk biseriate. Gynoecia not seen.

Differentiation and Variation—New Zealand representatives of the genus *Lepidozia* with margins of the leaf disc and lobes armed with discrete spines and/or cilia heretofore have been treated as a single species, *L. ulothrix*. In fact, in New Zealand, three distinct elements are represented: *L. ulothrix s. str.* (including *L. albula*), *L. kirkii*, and *L. hirta*. The first is broadly distributed in Australasia, the last two are endemic to New Zealand.

Lepidozia ulothrix is a robust plant, with distant, abbreviated, somewhat curved branches. The leaf armature of *L. ulothrix* is more copious than in *L. hirta*, with longer and more numerous spines, and/or cilia on the dorsal margin and confluent margin of the dorsal lobe, the lobe margins are armed with several, often opposing, spines, and the cells of the uniseriate row are more elongated.

The types of *Jungermannia ulothrix* and *J. albula* are somewhat less well developed than in some populations of the species, such as *Fife 8987*, which display a more pronounced development of armature on the dorsal leaf margin and lobes. These often have larger leaves with longer, more numerous (up to 19) cilia on the dorsal margin and confluent margin of the dorsal lobe, and leaf lobes with one to several pairs of opposing cilia, and terminating in a uniseriate row of as many as 14 cells.

More commonly the dorsal margin and the contiguous margin of the dorsal lobe bear only 11–13 cilia or teeth, those of the disc margin shorter than those of the lobe. Such plants may bear only 1–3 cilia of the dorsal lobe (Fig. 33 : 3–5), and these are only 6–7 cells long (Fig. 33 : 10, 11).

Distribution–Ecology—Auckland Is., New Zealand (South Is.), Tasmania, southeast Australia.

Known from scattered sites in the southern half of the South Island. In the Haast River area (sea level) the species occurs in mucky niches at the sides of mounds in open swampy areas with *Sphagnum* and scattered *Leptospermum*, etc. It is also present in the Cascade ultramafic moraine (S of Haast along Cascade Road), an area at low elevation (ca. 35–135 m) characterized by ultramafic rocks and outcrops with rather open vegetation consisting mainly of *Gleichenia, Lycopodium, Juncus,* the lichen *Cladina,* and scattered *Leptospermum;* at this site, the species is terricolous among Restionaceae. The plant from Bealey Glacier Track occurred at a considerably higher elevation, 915 m, at the bottom of an earth hummock, forming loose wefts over duff in a rain forest on a flat river terrace dominated by *Nothofagus solandri, Coprosma pseudocuneata, Dracophyllum longifolium,* and *Phyllocladus alpinus.*

Selected Specimens Seen—NEW ZEALAND. SOUTH ISLAND. WESTLAND PROV.: Cascade Road, Cascade ultramafic moraine, W of Martyr Saddle, SSW

of Jackson Bay, ca. 35 m, *Engel 21799* (F); ca. 4 km N of Haast River, sea level, *Engel 21769* (F). CANTERBURY PROV.: Arthur's Pass Natl. Park, Bealey Glacier Track, 915 m, *Fife 8987*—c. ♂ (F).

Subg. *Glaucolepidozia* Schust.

Lepidozia subg. *Glaucolepidozia* Schust., J. Hattori Bot. Lab. 36: 386. 1973 (1972).
Lepidoziopsis Hodgs., Rec. Domin. Mus. 4: 105. 1962.

Plants procumbent to creeping, forming thin, often extensive and pure, opaque, whitish patches, usually in deeply shaded sites. Similar to subg. *Notholepidozia* in the strongly incubously inserted and oriented leaves, but the leaves are usually only weakly convex and only slightly asymmetrically 4-lobed. Cells covered with an opaque whitish waxy substance, the leaf cells obscured, the cell walls difficult to resolve, even under the microscope. Plants not rigid, the stem not strongly corticated, usually regularly 1- or 1–2-pinnately branched; lateral branches all terminal, *Frullania* type.

TYPE—*Lepidozia glaucophylla* Steph.

The subg. *Glaucolepidozia* consists of four species that collectively are very distinctive in aspect. In the field, the plants look almost white and are quite opaque, owing partly to the peculiar cutinization, which is not seen in any other New Zealand hepatic. The strongly incubously inserted leaves are almost horizontally oriented, quadrate-oblong, and subsymmetrically 4-lobed, with edentate margins; they are much larger than the remote underleaves.

The subgenus is restricted to Australasia and occurs from Stewart Island north to North Island, at least to the Coromandel Peninsula. Plants are often found in areas shaded by shrubs or dwarfed trees, or in sheltered loci under ledges, at bases of shaded cliffs, or in pockets at tree bases. They are usually in diffuse but often extensive and very thin patches.

Both ecology and reproductive biology of *Glaucolepidozia* are distinctive. Three of the four taxa are known only sterile or from plants of one sex; only *L. glaucescens* is known with perianths. No taxon is known with sporophytes. In view of the rather wide distribution of several species and their rather regular occurrence in extensive mats in deeply shaded sites, their means of dissemination is of considerable interest. The species tend to occur on humus-rich soil or decayed wood in deeply shaded sites, such as hollows of decayed stumps, or on the ground on the shaded side of fallen and decayed trees. In at least *L. digitata,* weak forms may regularly have fragmenting or irregularly caducous leaf lobes (Fig. 38 : 1, 3, arrows), and even underleaf lobes may be caducous. Presumably dissemination is by such leaf fragments.

In *Glaucolepidozia,* leaf cells tend to show distinct middle lamellae (Fig. 38 : 10), and "Tangl's canals" may be evident (Fig. 36 : 9). In all taxa known from living plants, the chloroplasts are unusually dense and large (the whitish aspect is derived at least in part from reflection from chloroplast surfaces), and the oil-bodies are unusually small and often obscure (Figs. 36 : 9, 10; 38 : 9), always much smaller than the chloroplasts. They may be, in part, vestigial (Fig. 38 : 10) and formed of only 3–4 obscure segments. Stems, always creeping or procumbent, are relatively soft-textured; both cortical and medullary cells are virtually thin-walled (Figs. 36 : 11; 37 : 7).

Lepidozia glaucophylla (Hook. f. & Tayl.) G. L. & N. Figure 35

Jungermannia glaucophylla Hook. f. & Tayl., London J. Bot. 3: 580. 1844. *Lepidozia glaucophylla* (Hook. f. & Tayl.) G. L. & N., Syn. Hep. 207. 1845. *Mastigophora glaucophylla* (Hook. f. & Tayl.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. *Lepidoziopsis glaucophylla* (Hook. f. & Tayl.) Hodgs., Rec. Domin. Mus. 4: 106. 1962. Lectotype (*nov.*): Tasmania, 1840, *Hooker* (FH!).

Plants prostrate, in loosely interwoven pure mats or as conspicuous, isolated strands growing among other matted bryophytes, slender, with spreading branches, glaucous, whitish to ceraceous, the older sectors subnitid and brownish (as if scorched), the surface dull, waxy, and water repellent, the shoots medium, to 1.5 cm wide, including branches. Branching mostly of *Frullania* type, ± distantly 1(2)-pinnate, the branches gradually tapering, occasionally whiplike, flagelliform, and microphyllous, the nonmicrophyllous leaves subsymmetrically 4-lobed, the dorsal margin cordate at the base, the primary branches rarely developing into new leading shoots; secondary branches occasional in well-developed shoots; branch half-leaf broadly ovate, covering branch axil (as in *Bazzania*), slightly asymmetrical, cordate at base, 2-lobed to ca. 0.2–0.3, the margin sinuate or bluntly toothed; first branch underleaf large, mostly undivided, occasionally 2- or 3-

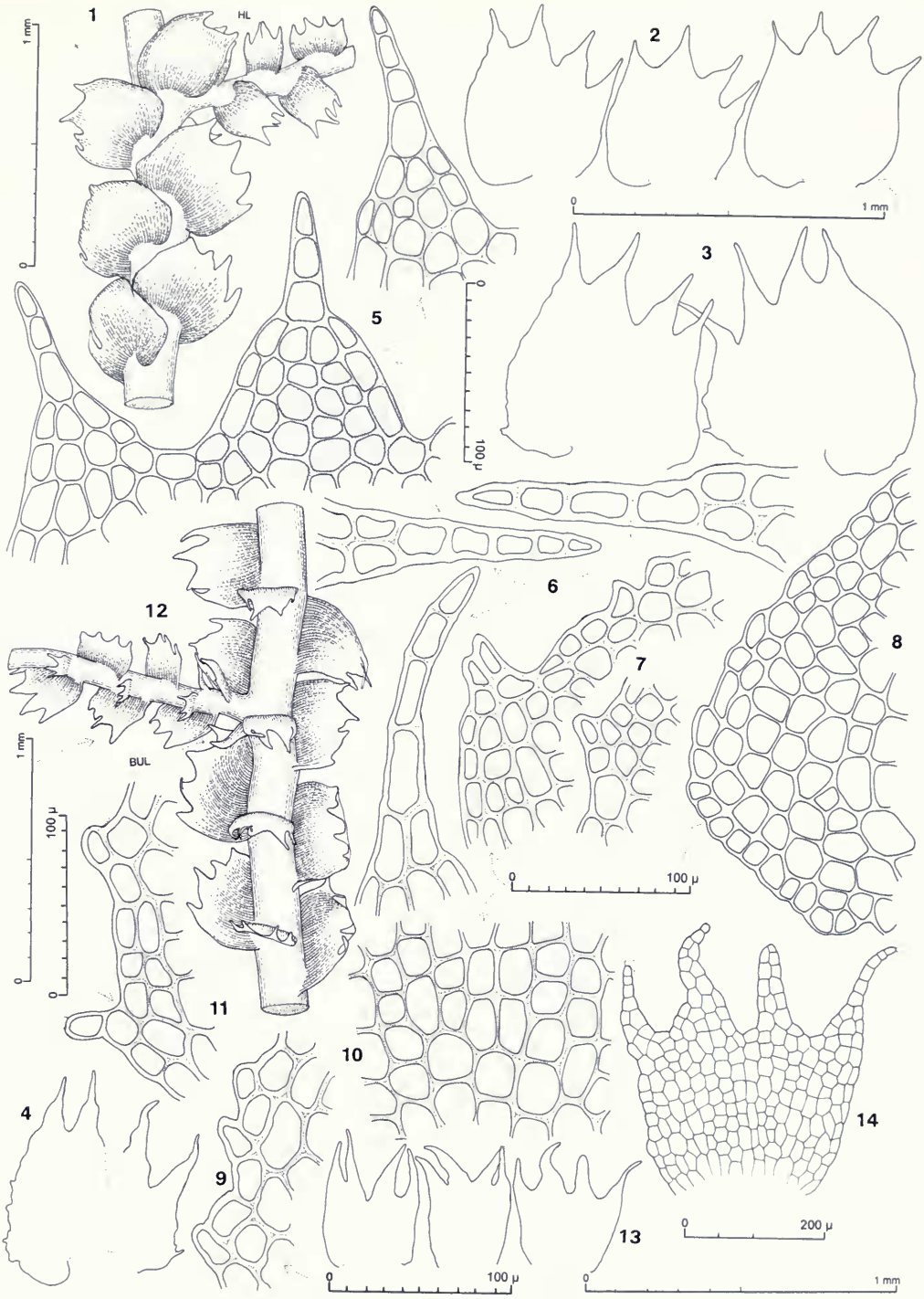

FIG. 35. *Lepidozia glaucophylla* (Hook. f. & Tayl.) G. L. & N. **1.** Sector of main shoot, dorsal view (HL = half-leaf). **2–4.** Leaves (all at same scale). **5.** Dorsalmost lobe (above) and dorsal pair of lobes, the cuticle shown for lobe at right. **6.** Median lobes of leaves (all at same scale). **7–9.** Marginal cells of ampliate sector (dorsal, basal portion) of leaf disc. **10.** Median disc cells. **11.** Portion of ventral margin of leaf disc. **12.** Sector of main shoot with *Frullania*-type branch, ventral view (note first branch underleaf, BUL). **13.** Underleaves. **14.** Underleaf, cellular detail. (Figs. 1, 2, 5, 8, 10, 12–14 from type; 3, 7 from *Fife 6442,* New Zealand, South Is., Paparoa Mts. Mt. Euclid; 4, 6, 9 from *Engel 23170,* New Zealand, South Is., Southland Prov., Fiordland Natl. Park, S end of Lake Marion.)

lobed, inserted on ventral-lateral side of branch at or near junction of branch and main shoot, typically obliquely to horizontally inserted and aligned with underleaves of branch. Ventral-intercalary branches sporadically produced. Stems flexuous. Stem epidermal cells in surface view ± thick-walled, with a waxy coating like that of the leaves, the stems 11–14 cells in diameter, the cortex in 1 layer of thin to slightly thick-walled cells ± distinctly larger than the medullary cells (the cortical cells well-defined in longisection, much shorter than the medullary); medullary cells slightly thickened. Leaves involute and subamplexicaul when dry, spreading and divergent when moist, rather strongly concave, contiguous to imbricate, at times nearly or completely hiding stem in dorsal view, uniform in size (not in sequential sectors of varying size), 0.6–0.7 mm long and wide, the insertion broad, moderately to strongly incubous, recurved at dorsal end; leaves asymmetrical, ± equally 4-lobed, the leaves divided to ca. 0.4–0.5 (median sinus), the distance from dorsal sinus base to insertion not much greater than that from ventral sinus to insertion, the sinuses gradually becoming deeper ventrally. Lobes subcaudate, not noticeably in pairs, entire, abruptly narrowing to a uniseriate row of 3–5(6) cells; cells of uniseriate row and often the subtending lobe cells elongated (to 2:1), thick-walled, the terminal cell tapering to a point; dorsal lobe 5–7 cells wide at base. Disc distinctly asymmetrical because of ampliation of dorsal margin, the dorsal sector to one-third the disc area, 14–18 cells high at dorsal sinus, 10–14 cells high at ventral sinus, the dorsal margin subentire to sinuate to distantly and irregularly armed with 1–2-celled teeth, the margin auriculate at the base, the ventral much shorter than the dorsal, subcordate at the base, occasionally with a small tooth or short spine. Cells of disc and lobes rounded quadrate, evenly thick-walled, trigones absent, the median disc cells 20–26 μm × 22–30 μm; marginal cells of disc and lobes typically with a thickened outer wall; cuticle a dense and coarsely granular coating. Underleaves inserted on 8–9 rows of stem cells, distinctly spreading, ca. 1–1.3× stem width, symmetrically 4-fid to ca. 0.4 (median sinus), the lobes plane, entire, narrowly attenuate and consisting of several tiers of 2 laterally juxtaposed cells and then rounded at the tip or, more commonly, terminating in a uniseriate row of 2–4 cells; disc 9–12 cells high at median sinus, the margins plane, occasionally with a 1–2-celled tooth that terminates in a slime papilla.

Androecia and gynoecia not seen.

DIFFERENTIATION—*Lepidozia* species with a waxy, water-repellent "bloom" on the surface of the stems and leaves have been understood as constituting a single species, *L. glaucophylla.* Primarily because of this striking feature, the species has been treated as the type of a monotypic genus, *Lepidoziopsis* Hodgs. Schuster (1973) listed a number of additional distinctive features of this taxon, which he treated as *Lepidozia* subg. *Glaucolepidozia* Schust. In fact, in New Zealand, four distinct elements are represented: *L. glaucophylla* s. str., *L. bisbifida* Steph., *L. digitata* Herz., and *L. glaucescens,* described here.

Examination of the Tasmanian type of *Lepidozia glaucophylla* (FH!) shows it to be distinct from the familiar New Zealand plant that has long been known by this name. True *L. glaucophylla* appears to be the only species of this complex present in Tasmania and Australia, but it is quite rare in New Zealand; *L. bisbifida* Steph. (apparently the oldest name for the New Zealand plant) is "widely distributed in New Zealand, but nowhere common" (Allison & Child, 1975, p. 65) and is probably endemic.

Lepidozia glaucophylla is similar to *L. bisbifida* in the conspicuous water-repellent "bloom" on the surface of the stem and leaves and the strongly incubous, subsymmetrically lobed leaves (Fig. 35 : 1–3). It is immediately distinguishable, however, by the broadly ampliate and strongly auriculate dorsal margin of the leaf (Fig. 35 : 1–4, 8); the irregularly sinuate to toothed leaf margins (Fig. 35 : 7–9); the evenly thick-walled disc cells (Fig. 35 : 7, 9, 10); the subcaudate, abruptly tapering leaf lobes, which terminate in a uniseriate row of 3–5 elongated cells (Fig. 25 : 4–6); and the oblique to longitudinal insertion of the first branch underleaf at the base of the branch, rather than transversely inserted on the ventral-lateral face of the stem, as in *L. bisbifida.*

DISTRIBUTION–ECOLOGY—New Zealand, Tasmania, Australia (Victoria, N. S. W.). Apparently very rare in New Zealand, and known only from a few sites on South Island. The Engel plant occurred at 695 m in a rather open forest dominated by *Nothofagus menziesii,* with frequent large boulders that are often largely bryophyte covered. Plants of *L. glaucophylla,* together with hymenophylls, formed a thick mass that was loosely attached to a huge boulder; the boulder otherwise was covered with bryophytes and hymenophylls. Interesting ecological partitioning occurred here:

Lepidozia bisbifida occurred on soil of the forest floor deep in a recess formed by a ledgelike overhang of the same boulder. The Fife plant occurred on humus over rock in a north-facing, moist *Nothofagus menziesii* forest with abundant *Dracophyllum traversii* at 1000–1065 m.

SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Fiordland Natl. Park, S end of Lake Marion, W of Hollyford River, 695 m, *Engel 23170* (F). NELSON PROV.: Paparoa Mts., N flank of Mt. Euclid, ca. 0.5 km SE of Morgan Tarn, 1000–1065 m, *Fife 6442* (F).

Lepidozia bisbifida Steph. Figure 36

Lepidozia bisbifida Steph., Spec. Hep. 3: 593. 1909. Original material: New Zealand, without specific locality, *Kirk s.n.* (G!).

Lepidozia subquadrata Steph., Spec. Hep. 6: 341. 1922. Original material: New Zealand, "alpine interior," without specific locality, *Colenso "inter 2064"* (G!).

Lepidozia brevipinna Pears., Univ. Calif. Publ. Bot. 10: 321. *pl. 94.* 1923. Original material: New Zealand, North Is., Wairakei, Waiora Valley, 4 May 1904, *Setchell 9* (UC!).

Plants prostrate to loosely procumbent, the stems loosely interwoven, flexuous, with spreading branches, glaucous and ash-gray to ivory, the older shoot sectors burnt orange or lightly tinged with brown as if scorched, the surface dull and water repellent; shoots medium-sized, to 1.5 cm wide, including branches (sporadically large and to 2 cm wide [including branches] × 7.5 cm long). Branching nearly exclusively of *Frullania* type, rather short, closely and regularly pinnate to locally bipinnate, the branches abruptly tapering, occasionally becoming ± whiplike, flagelliform, and microphyllous, the nonmicrophyllous leaves shallowly and ± symmetrically 4(5)-lobed, the primary branches sometimes developing into new leading shoots; secondary branches occasional, 1–3 per primary branch; branch half-leaf broadly ovate, covering branch axil (as in *Bazzania*), subsymmetrical, subcordate at the base, 2-lobed to ca. 0.2–0.3, the dorsal lobe often smaller; first branch underleaf large, often squarrose reflexed, 2–4-lobed (rarely undivided), usually transversely inserted on lateral or ventral-lateral side of stem, often somewhat below the branch, aligned with leaves of main shoot or underleaves of branch. Ventral-intercalary branching occasional, leafy. Stems flexuous. Stem epidermal cells thin-walled, with a waxy coating like the cells of the leaves. Leaves involute-triangular and distinctly amplexicaul when dry, when moist rigid, distinctly concave to nearly cuplike, approximate to contiguous, intermittently large and small along length of stem, those in well-developed sectors 0.8–1.3 mm long and wide, the leaves of smaller sectors as small as 0.5 mm long and wide, the leaves spreading, nearly horizontal, the insertion broad, strongly incubous, recurved at dorsal end; leaves subsymmetrical to moderately asymmetrical, typically ± equally 4-lobed (rarely bisbifid), the lobes sometimes in turn divided, the leaves then appearing 5–8-lobed, the leaves divided to ca. 0.2–0.5 (median sinus), the distance from dorsal sinus base to insertion subequal to or not much greater than that from ventral sinus to insertion, the sinuses of subequal depth or gradually becoming deeper ventrally. Lobes acute to apiculate, entire, terminating in a single cell or more commonly a uniseriate row of 2–3 cells; cells of uniseriate row ± isodiametric or slightly longer than wide, thin-walled, the terminal cell strongly tapering; median pair of lobes somewhat larger, 6–8(11) cells wide at base, the dorsal lobes (2)3–5 cells wide at base. Disc subsymmetrical, (13)15–22(28) cells high at dorsal sinus, 9–14 cells high at ventral sinus, the margins usually entire, the dorsal margin moderately ampliate, sporadically with 1 or more blunt teeth or sinuate, cordate at the base, the ventral margin not much shorter than the dorsal, occasionally with a slender lobuliform process. Cells of disc and lobes uniformly thin-walled, with conspicuous intercellular pits, trigones minute to medium, the median disc cells (18)24–40 × 28–40 μm; median basal cells not differentiated; marginal cells of disc smaller, those of disc and lobes sporadically with thickened outer walls, but rarely consistently so; cuticle a dense granular coating that ultimately develops cracks or fine fissures (especially over the vertical cell walls), the cell outlines obscured by the scurfy, water-repellent coating. Oil-bodies small and inconspicuous, 2–5 to (0)4–6(9) per cell, few (often only 3–6[9]) segmented, coarsely botryoidal, much smaller than chloroplasts, often 6 μm long × 3 μm wide and consisting of a large spherule at each end and 4–6 smaller ones centrally. Underleaves inserted on 9–10 rows of stem cells, widely spreading, ca. 0.7–1× stem width, asymmetrically or symmetrically 4-fid to ca. 0.3–0.45 (median sinus), the underleaves often with 1, 2, or all 3 sinuses narrow, slitlike and the lobes adnate by the surface covering, the underleaves then in situ appearing 2 or 3 lobed, the lobes plane, entire, attenuate to acuminate, consisting of serveral tiers of 2 later-

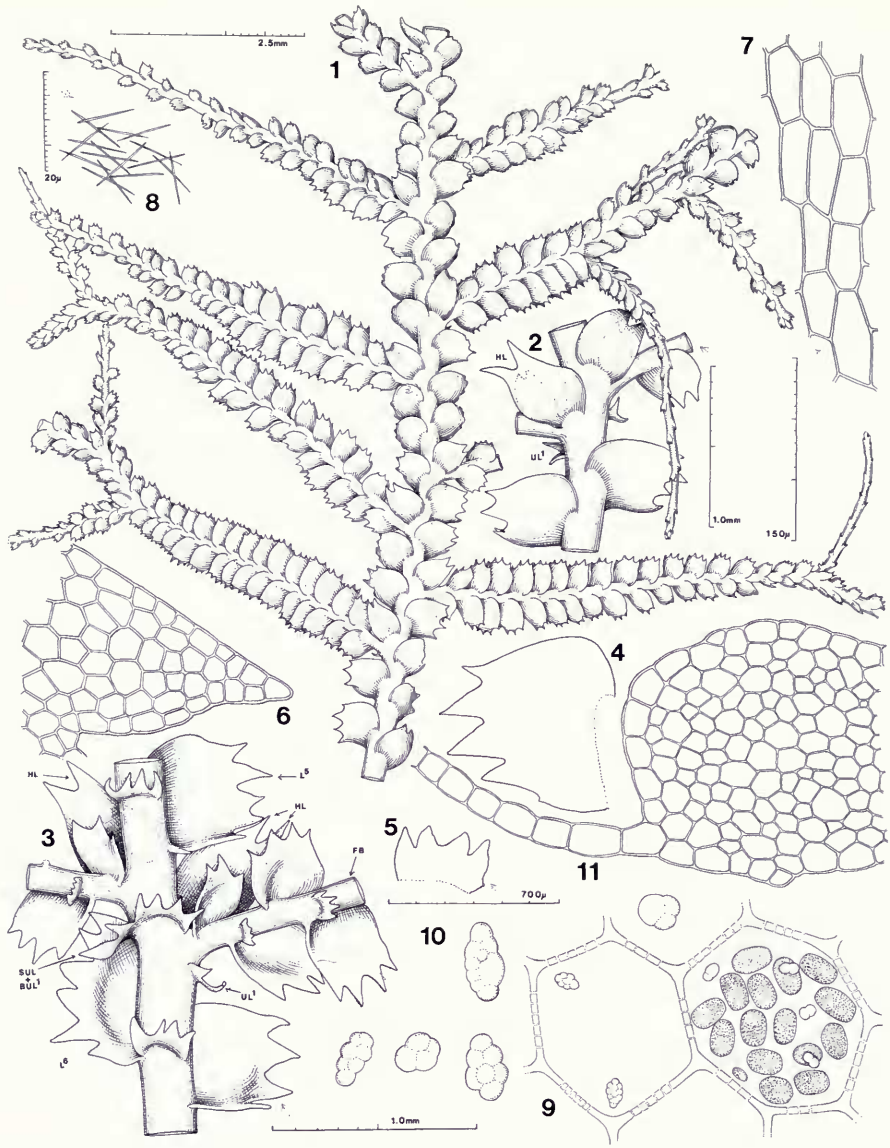

FIG. 36. *Lepidozia bisbifida* Steph. **1.** Part of plant, dorsal aspect (×10.2; 2.5 mm scale). **2.** Sector of main stem, dorsal view; half-leaf (HL) and first branch underleaf (UL^1) labeled (×21; 1.0 mm scale). **3.** Same, ventral aspect; lateral leaves in part 5-lobed (L^5), in part 6-lobed (L^6); *Frullania*-type branches (FB) with basal branch underleaf at right (UL^1) inserted below seeming branch base; at left, stem underleaf (SUL) and branch underleaf (BUL^1) faintly connate at juxtaposed bases (×27; lower 1.0 mm scale). **4, 5.** Stem leaf and underleaf (×32; 700 μm scale). **6.** Leaf lobe cells (×160; 150 μm scale). **7.** Cortical cells (×160; 150 μm scale). **8.** Raphides (×650; 20 μm scale). **9.** Cells with oil-bodies; right, chloroplasts (×190). **10.** Oil-bodies (×190). **11.** Stem cross section (×190).

ally juxtaposed cells and then rounded at the tip or, more commonly, terminating in a single cell or a uniseriate row of 2–4 cells that often terminate in a slime papillae; disc 5–9 cells high at median sinus, the margins plane, entire.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, often cernuous ventral-intercalary branches from main shoot; bracts ventricose-cucullate, 2-lobed to ca. 0.3, the lobes acute to short acuminate; dorsal margin of disc dilated in basal sector to form a feebly to moderately rounded projection, the dilated portion

crenulate and with several slime papillae, the disc otherwise entire; antheridia 1 per bract, the stalk biseriate. Gynoecia not seen.

DIFFERENTIATION—This is the species long known in the New Zealand literature as *L. glaucophylla*; for the correct application of this name, see the discussion under that species. *Lepidozia bisbifida* is readily distinguished from *L. glaucophylla* by the broadly inserted, deeply concave, involute leaves (Fig. 36 : 1); by the leptodermous leaf cells with small to minute trigones (Fig. 36 : 9); and by the ± transverse insertion of the first branch underleaf on the stem, often some distance below the associated branch (Fig. 36 : 3). The thin walls of the leaf cells are traversed by delicate intercellular connections (plasmodesmata, Fig. 36 : 9). Another feature of this species is the variability in leaf size on a single shoot and the characteristic appearance of the branches (Fig. 36 : 1), which are abruptly tapering and have much smaller leaves than those of the main shoot. The first branch underleaves in this species are inserted well below the apparent branch base (Fig. 36 : 2, 3).

The marginal cells of disc and lobes are typically thin-walled like those of the leaf interior. Marginal cells, however, sporadically have thickened outer walls and at times these may be locally feebly crescentic. In *Engel 22930* the marginal cells of both disc and lobes have strongly thickened, concave outer walls, with the wall thickening crescentic and bulging into the cell lumen.

In water mounts, the waxy, granular coating on the leaf surface renders the leaves almost opaque and obscures the outlines of the cells. An interesting feature of the species is the fine network of hairline cracks in the cuticle, which is visible over the cell walls of dried specimens. When the leaves are mounted in Hoyer's solution, the waxy coating is apparently dissolved and forms delicate, needle-like crystals (Fig. 36 : 8).

DISTRIBUTION–ECOLOGY—Confined to New Zealand (South Is., North Is., Antipodes Is.).

A species occurring in forests ranging from as low as 450 m, but more often from over 750 m to the upper reaches of the forest. It is found on rotted wood (particularly where there is cover of other bryophytes, along with, at times, hymenophylls) or deep in shaded, moist, sheltered pockets of tree bases, boulders (see also note under *L. glaucophylla*), or rotted logs. Also on shaded cliff bases, particularly where soil has accumulated, and plants are notable as scattered glaucous patches among other bryophytes. The species at times covers large areas but typically does not become matted or pure. However, pure mats are at times formed deep in sheltered recesses. In the subalpine zone over soil deep in protected recesses between boulders or under boulder overhangs, as well as on the sides of rills. In the alpine zone on shaded, damp slopes under cover of snow tussock.

This is the only species of subg. *Glaucolepidozia* known from the geothermal areas of North Island, New Zealand. The presence of *L. bisbifida* at such sites is somewhat of an anomaly, because higher plants from geothermal areas are for the most part cosmopolitan plants of the tropics; moreover, few or no higher plants are endemic to geothermal areas. Rather, they are weedy in nature, high light loving, and, if they occur elsewhere in New Zealand, they typically are present only in warm sites, such as in the vicinity of Auckland or Northland (J. Braggins, pers. com.). All of the specimens of *L. bisbifida* cited here from geothermal areas are from, at least to some degree, shaded sites; the Braggins plant, for example, occurred in light shade under *Kunzea*.

The species is quite distinct in the field due to the large plant size coupled with the glaucous condition, with older portions of the plants often burnt orange or lightly tinged with brown and then appear as if scorched. It often grows loosely attached, and may be very common locally, such as at the Moraine Creek Track site.

SELECTED SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Fiordland Natl. Park, off track to Island Lake, just W of Borland Saddle, S of South Branch of Borland Burn, W of Monowai, 800 m, *Engel 18621* (F); ibid., Central Earl Mts., Mistake Creek, between Triangle Peak and Melita Peak, NE of northern end of Lake Te Anau, 740–800 m, *Engel 18784* (F); ibid., Gertrude Valley, near track entrance to Gertrude Saddle, E of Homer Tunnel, 1740 m, *Engel 21947* (F); ibid., S end of Lake Marion, W of Hollyford River, 695 m, *Engel 23168* (F); Lake Marian Valley, ca. 305 m, *Child H2950* (F); Fiordland Natl. Park, Moraine Creek Track, area N of Moraine Creek, W of Hollyford River, 610 m, *Engel 23227* (F). SOUTHLAND/OTAGO PROV. BOUNDARY: Lake Howden, ca. 760 m, *Child 2557* (F). OTAGO PROV.: Ajax Swamp, ca. 1 km N of Ajax Hill, Catlins River area, ca. 610 m, *Child H5494* (F); Mt. Cargill, N of Dunedin, ca. 455 m, *Child H1706A* (F); Rees Valley, Invincible Creek, ca. 455 m, *Child H375* (F); tributary of Siberia Stream, opposite and downstream from Siberia Hut, WNW of Makarora, ca. 760 m, *Child H2873* (F); Fiordland Natl. Park, near McKerrow Hut, head of Lake McKerrow, *Hatcher 1446* (F); Mt. Aspiring Natl. Park, below and W of Mt. Shrimpton, 1370–1470 m, *Engel 17880* (F); ibid., Blue Valley Track, above Blue River just N of confluence with Makaroa River, 430–480 m, *Engel 21908* (F). OTAGO/WESTLAND PROV. BOUNDARY: Mt. As-

piring Natl. Park, Cross Creek, 1 km N of Haast Pass, 510 m, *Engel 23105* (F); ibid., summit area of Haast Pass, 570 m, *Engel 17986* (F); Mt. Brewster, ca. 1370 m, *Child 4188* (F). WESTLAND PROV.: 2 km N of White Horse Creek, ca. 305 m, *Child H5425* (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Arthur's Pass, near Temple Basin Ski area, *Engel 6499A* (F); ibid., Bridal Veil Track, E side of Bealey River and just N of town of Arthur's Pass, 760–825 m, *Engel 22930* (F). CANTERBURY PROV.: Cass, Woolshed Hill, *Visch s. n.* (F); Arthur's Pass Natl. Park, Bealey River, off Bealey Valley Track, 830–850 m, *Engel 18516—c.* ♂ (F). NELSON PROV.: Paparoa Mts., N flank of Mt. Euclid, ca. 0.5 km SE of Morgan Tarn, *Fife 6412, 6442* (F). NORTH ISLAND: WELLINGTON PROV.: Tongariro Natl. Park, Blyth Track, along small stream ca. 0.5 km from Ohakune Mt. Road, ca. 1230 m, *Engel 21310* (F); Tokaanu Hot Springs, S end of Lake Taupo, *Braggins—c.* ♂ (F). SOUTH AUCKLAND PROV.: Rotorua thermal area, *Hatcher 36* (F); ibid., *Barnard NZ-24* (F). ANTIPODES ISLAND: ca. 150 m, *Godley* (F).

Lepidozia digitata Herz. Figures 37 and 38

Lepidozia digitata Herz., Trans. & Proc. Roy. Soc. New Zealand 68: 45. *pl. 5, m-n.* 1938. Holotype: New Zealand, near Atiamuri, *Allison 72* (JE!).

Plants with the superficial facies of *Telaranea centipes,* prostrate, the stems loosely interwoven, flexuous, with widely spreading branches, glaucous to ivory, the older shoot sectors tinged with brown, the surface dull and water repellent; shoots small, to 0.6 cm wide, including branches. Branching exclusively of *Frullania* type, the branches rather short, rather distant and irregularly pinnate, the branches short and not tapering or only sporadically becoming flagelliform and microphyllous, the nonmicrophyllous leaves ± symmetrically (3)4-lobed, to 3-lobed in distal sectors; branch half-leaf narrowly ovate, subsymmetrical, subcordate at the base, 2-lobed to ca. 0.2–0.3; first branch underleaf 2-lobed (occasionally undivided), inserted on ventral-lateral side of main shoot at branch base and obliquely to subvertically inserted. Ventral-intercalary branching not seen. Stems flexuous. Stem epidermal cells thin-walled, with a waxy coating like the cells of the leaves, the cortex in a single row of cells that are slightly smaller to or at most feebly larger than those of the medulla. Leaves with margins somewhat involute when dry, plane to slightly concave when moist, distant to contiguous, ± uniform in size, 0.35–0.55 mm wide × 0.4–0.55 mm long, spreading, nearly horizontal, the insertion broad, strongly incubous, at most feebly recurved at dorsal end; leaves at most moderately asymmetrical, (3)4-lobed to ca. 0.35 (median sinus), the distance from dorsal sinus base to insertion not much greater than that from ventral sinus to insertion, the sinuses gradually becoming deeper ventrally. Lobes subacuminate, entire, terminating in a uniseriate row of 2–3(4-5) cells; cells of uniseriate row ± isodiametric or somewhat longer than wide, thin-walled, the terminal cell tapering to a rounded apex; median pair of lobes somewhat larger, 3–5(6) cells wide at base, the dorsal lobe 2–3(4) cells wide at base. Disc subsymmetrical, (6)7–13(16) cells high at dorsal sinus, 6–13 cells high at ventral sinus; dorsal margin scarcely ampliate, entire or somewhat sinuate, sporadically with a 1-celled tooth, feebly cordate at the base; ventral margin somewhat shorter than the dorsal, entire. Cells of disc and lobes uniformly thin-walled, trigones none or minute, the median disc cells 24–35 μm wide × 29–42 μm long; median basal cells somewhat elongated but otherwise not differentiated; marginal cells of disc (especially the dorsal) often with a somewhat thickened, concave outer wall (the wall thickening somewhat crescentic and bulging into the cell lumen); cuticle finely granular, the cell outlines obscured by the scurfy, water-repellent coating. Oil-bodies small or tiny, in some cells rudimentary (and obscurely few-septate), much smaller than chloroplasts, very variably developed, ranging from tiny and few-septate to ellipsoidal or fusiform and clearly botryoidal. Underleaves inserted on 3–4 rows of stem cells, small, slightly spreading, ca. 1–1.3× stem width, ± symmetrically 3–4-fid to ca. 0.5–65 (median sinus), the sinuses broad to narrow, the lobes entire, slender, 2–3(4) cells wide at the base and often uniseriate for most of their length, the uniseriate row of 2–3 cells and often terminating in a slime papilla; disc (1.5)2–4 cells high at median sinus, the margins plane, entire. Asexual reproduction sporadically present, via fragmenting or caducous leaf lobes, in which bases persist as truncate stubs.

Androecia and gynoecia not seen.

DIFFERENTIATION—*Lepidozia digitata* is the smallest of the four New Zealand species of subg. *Glaucolepidozia,* with leaves at most 0.5 mm in longest dimension. Hodgson (1956) treated *L. digitata* as a small-leaved expression of "*L. glaucophylla*" (i.e., *L. bisbifida*), but it differs in being only one-third the size. The leaves are uniformly small, not in alternate sectors of large and small leaves along the length of the stem as in *L. bisbifida.* Curiously, Herzog (1938), who described

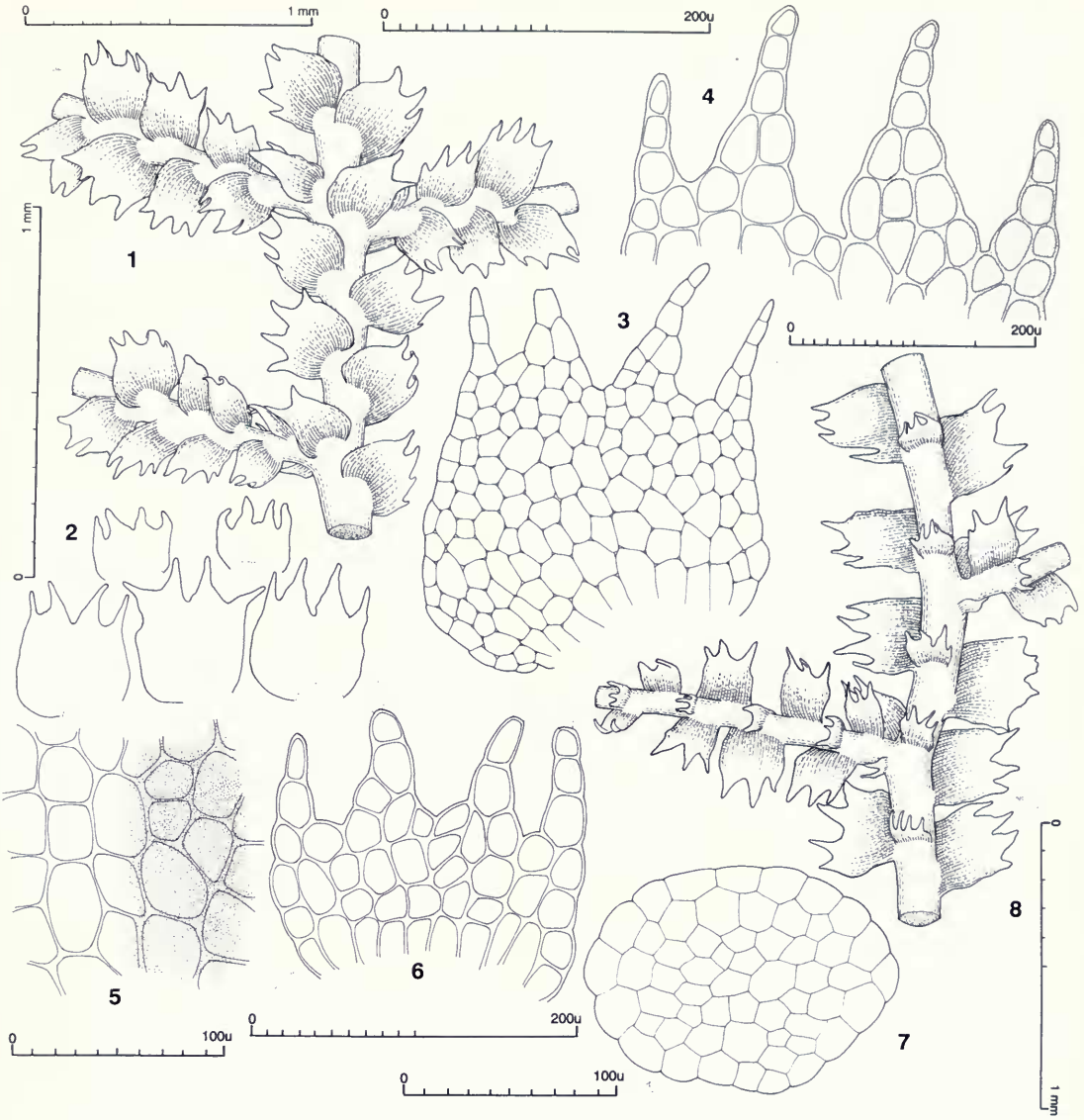

FIG. 37. *Lepidozia digitata* Herz. **1.** Sector of main shoot, dorsal view. **2.** Leaves and, above, underleaves. **3.** Leaf, cellular detail. **4.** Leaf lobes, cuticle indicated in part. **5.** Median disc cells, cuticular detail indicated in part. **6.** Underleaf, cellular detail. **7.** Stem, cross-section. **8.** Sector of main shoot with 2 *Frullania*-type branches, ventral view (note undivided and, lower, bilobed first branch underleaves; the latter is the typical condition). (All from type.)

the leaf cells as "subopaco–brunneolae" and the cuticle as "minutissime et densissime punctulata," did not associate this species with *L. glaucophylla;* the type is distinctly glaucous and water repellent.

Lepidozia digitata is not only the smallest species of *Glaucolepidozia,* it has the most remote leaves (Figs. 37 : 1, 8; 38 : 3). It apparently reproduces only via fragmenting leaf lobes, in which bases persist as truncated stubs. Such asexual reproduction may be widespread (Fig. 38 : 1, 3) or sporadically evident (Fig. 37 : 8). The leaf lobes mostly end in 3 superposed cells (Fig. 37 : 3, 4) but on weak phases sometimes in 4–5 cells (Fig. 38 : 1, 4, 6). Underleaves on branches or (weak phases) even on main stems may be bifid or trifid in part, or predominantly so (Figs. 37 : 8; 38 : 3). Although the disc may be 3–4(5) cells high on

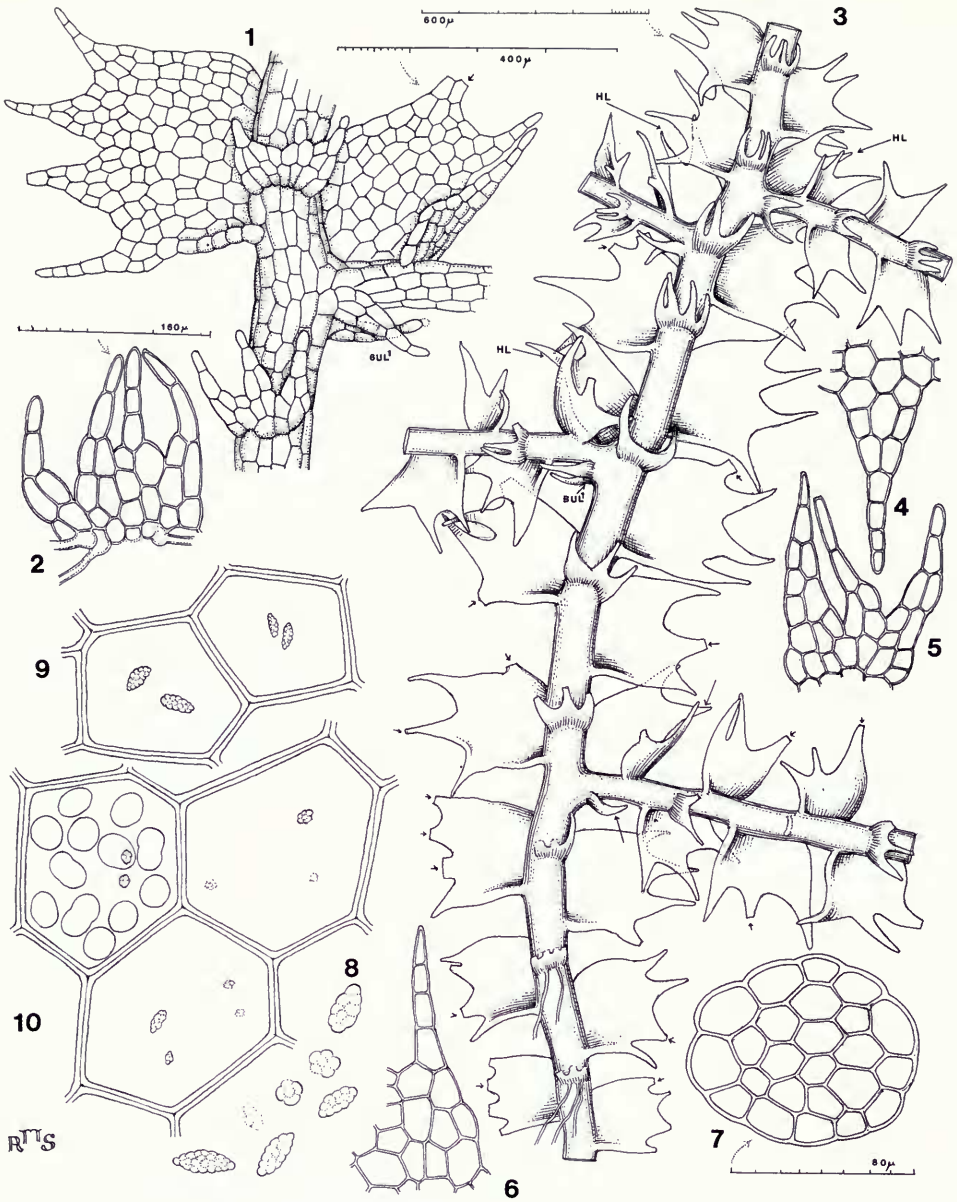

FIG. 38. *Lepidozia digitata* Herz. **1.** Shoot sector, ventral aspect; at right, a *Frullania*-type branch, with bifid first branch underleaf (BUL¹) (×93; 400 μm scale). **2.** Underleaf from stem (×170; 150 μm scale). **3.** Part of plant, ventral aspect; of the four *Frullania*-type branches, the upper three bear bifid first branch underleaves, the lower (arrow) a monocrural one; at arrows, leaf lobes that have fragmented (×50; 600 μm scale). **4.** Median lobe of leaf (×170; 150 μm scale). **5.** Underleaf (×170; 150 μm scale). **6.** Ventral lobe of leaf (×170; 150 μm scale). **7.** Stem cross section (×300; 80 μm scale). **8.** Individual oil-bodies (×1770). **9.** Two cells with oil-bodies (×925). **10.** Three laminar cells with oil-bodies; at, upper left, chloroplasts (×925). (All from *Schuster 95-314,* New Zealand, North Is., Urewera Natl. Park; FAA preserved plants.)

vigorous phases, weak phases may have it only 2–3 cells high (Fig. 38 : 2). Stems are weaker in *L. digitata* (compare Figs. 37 : 7 and 38 : 7 with Fig. 36 : 11, *L. bisbifida*) than in other *Glaucolepidozia* species; on weak phases they may be only 6 cells high, ranging to 8–9 cells high in vigorous phases. Oil-bodies in this species are often vestigial (stippled ones in Fig. 38 : 8, 10 are almost

unresolvable, even under oil immersion) and typically occur only 2–4 per cell; they are often obscured by the large, often dense chloroplasts.

DISTRIBUTION–ECOLOGY—New Zealand (South and North Is.).

The few, scattered stations for the species are for the most part within *Nothofagus solandri* var. *cliffortioides* and *Nothofagus menziesii* forests ranging from 630 to 1390 m. It occurs in shaded, protected, often deep pockets (such as the hollowed recesses of tree bases); in crevices and recesses of outcrops; or over soil of steep, mossy banks, where it may occur, for example, in a protected niche under the lip of the forest edge at the upper extremity of a stream bank (*Engel 22637*). Also known from 455 m in Otago Prov. (Invincible Creek, leg. *Child*); the vegetation type is not provided.

SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. OTAGO PROV.: Rees Valley, Invincible Creek, ca. 455 m, *Child H375* (F). CANTERBURY PROV.: Arthur's Pass Natl. Park, Scotts Track to Avalanche Peak, W of town of Arthur's Pass, 950 m, *Engel 22081* (F). NELSON PROV.: Nelson Lakes Natl. Park, Pinchgut Track, W of southern sector of Lake Rotoiti, SSW of St. Arnaud, ca. 1280–1390 m, *Engel 21424* (F); ibid., off Lakehead Track, near juncture with southern end of Loop Track, NE end of Lake Rotoiti, 630 m, *Engel 22637* (F). NORTH ISLAND, WELLINGTON PROV.: Tongariro Natl. Park, west-facing steep bank of Mangawhero River, off Ohakune Mt. Road, ca. 1200 m, *Engel 21287* (F). GISBORNE PROV.: Urewera Natl. Park, Huiarau Range, summit area of Te Rangaakapua, 1230–1320 m, *Engel 23470* (F).

Lepidozia glaucescens Engel, sp. nov. Figure 39

Folia infirme vel distincte incuba insertione angusta exorientia, distincte asymmetrica, margine dorsali subrecta et disco plano et lobis patentibus praedita; cellulae et disci et loborum foliarium parietibus distincte crassis, papillis striatis, velamineque continuo ceraceo granuloso instructae.

HOLOTYPE—New Zealand, South Island, Nelson/Westland Prov. boundary, Porarari River Track, 5 km from road, ca. 500 ft., *Child H4966* (F); isotype: (CHR).

Plants prostrate, in loosely interwoven mats, the shoots slender, fragile, with widely spreading branches, fragile, brownish and subnitid to glaucous and ivory-white (at least on new growth), the surface then dull and water repellent, the shoots medium, to 2.5 cm wide, including branches. Branching nearly exclusively of *Frullania* type, ± regularly 1-pinnate varying to remotely 2-pinnate, the branches gradually tapering, becoming whiplike, flagelliform and microphyllous, the nonmicrophyllous branch leaves ± symmetrically 4-lobed, the 2 median lobes somewhat larger, the primary branches occasionally developing into new leading shoots; secondary branches sporadic, 1–2 per primary branch; branch half-leaf narrow, linear, subsymmetrical, subcordate at the base, 2-lobed to ca. 0.4; first branch underleaf mostly undivided, less commonly 2(4)-lobed, inserted on ventral-lateral side of branch base and aligned with underleaves of branch. Ventral-intercalary branching rare, leafy. Stems flexuous. Stem epidermal cells in surface view rather thick-walled, sometimes with a waxy coating like that of the leaves. Leaves fragile, when dry moderately concave, with the lobes curved ventrally; leaves when moist explanate, with spreading lobes, ± distant to contiguous, with much of stem visible in dorsal view, uniform in size (not in sequential sectors of varying size), narrowly inserted and somewhat longer than wide, 0.3–0.5(0.6) mm long and wide, spreading, the insertion varying from weakly to distinctly incubous; leaves moderately to distinctly asymmetric, unequally 4-lobed, the leaves divided to ca. 0.4–0.55 (median sinus). Lobes narrowly attenuate to acuminate, the dorsal lobes ± paired, the ventral shorter than the dorsal lobes and somewhat divergent, the lobes entire, terminating in a uniseriate row of 3–4(5) cells; cells of uniseriate row isodiametric to ± elongated (to 2:1), thick-walled and often with somewhat swollen septa, the terminal cell often moderately to distinctly elongated, tapering to a point; the dorsal lobe 3–4(5) cells wide at base; cuticle of lobes striate papillose, the papillae mostly obscured by the thin and continuous granular coating. Disc moderately to distinctly asymmetrical, obliquely truncate and deltoid, 8–12 cells high at dorsal sinus, 5–9 cells high at ventral sinus; dorsal margin ± straight, abruptly cordate at the base, entire; ventral margin shorter than the dorsal, at times distinctly so, entire. Cells of disc middle thick-walled, with trigones small, the cells somewhat longitudinally elongated, 18–24(28) μm wide × 21–30 μm long, the cells of the narrow dorsal sector smaller and quadrate; median basal cells in 1 (locally 2) rows of enlarged cells; marginal cells of disc and lobes typically with a thickened outer wall (the wall thickening often crescentic and bulging into the cell lumen); cuticle of disc as in lobes. Underleaves inserted on 4–6 rows of stem cells, spreading, small, ca. 0.9–1×

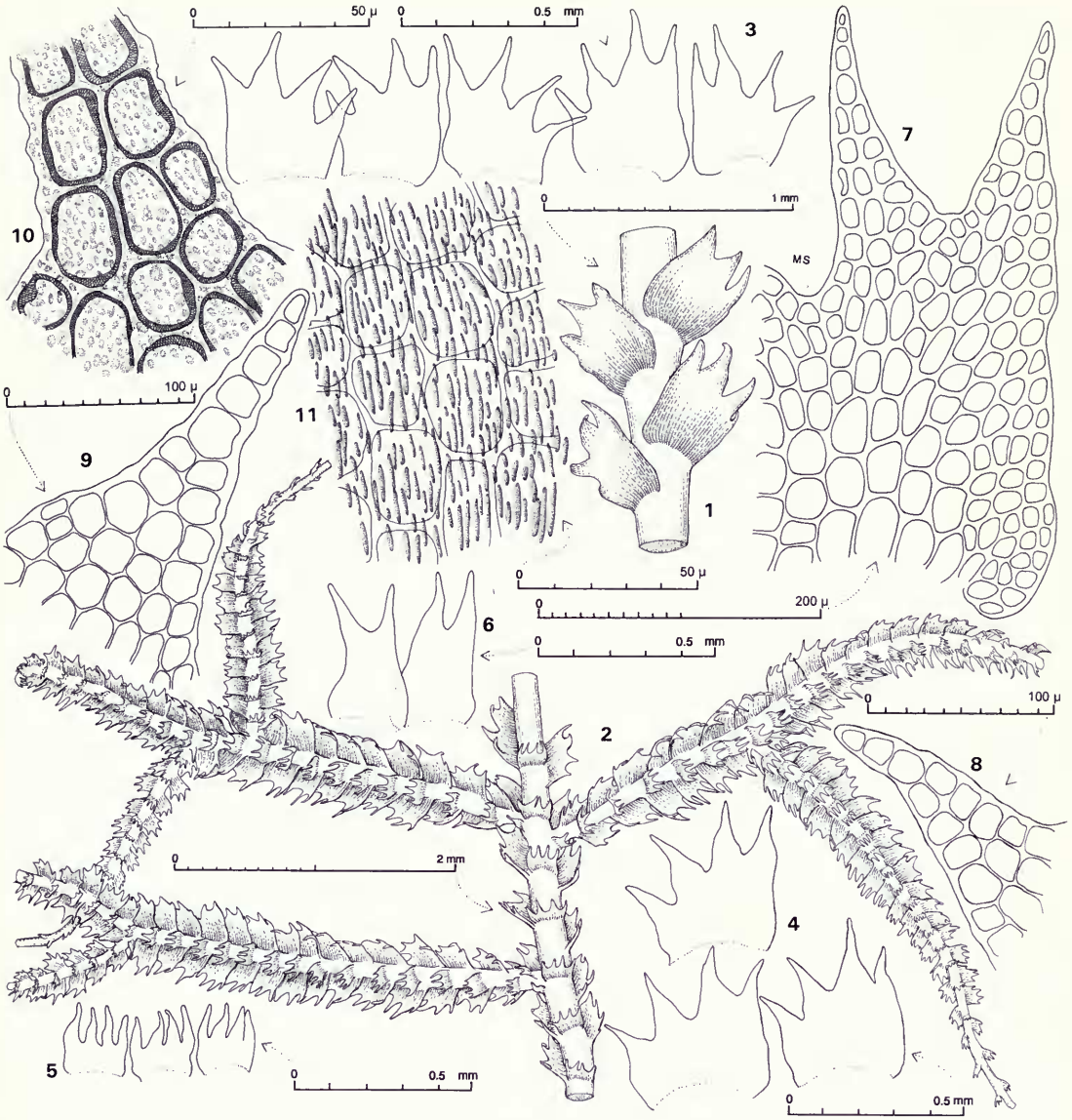

FIG. 39. *Lepidozia glaucescens* Engel. **1.** Sector of main shoot, dorsal view. **2.** Sector of main shoot, ventral view. **3, 4.** Leaves. **5.** Underleaves. **6.** Half-leaves. **7.** Dorsal half of leaf (ms = median sinus). **8.** Outer (dorsalmost) lobe of dorsal half of leaf (cuticular detail not shown). **9.** Median lobe of dorsal half of leaf (cuticular detail not shown). **10.** Portion of dorsal lobe showing cuticular papillae, granular coating, and lamellated cell walls (cross-hatched shading). **11.** Median cells of dorsal half of disc showing striate cuticle. (Figs. 1–3, 5–7, 10 from type; 4, 8, 9, 11 from *Engel 21087,* New Zealand, North Is., North Auckland Prov., SE corner of Waipoua Forest.)

stem width, symmetrically 4-fid to 0.5 (median sinus), the lobes plane, slenderly acuminate, entire, terminating in a uniseriate row of 2–3(5) cells; disc 3–6 cells high at median sinus, the margins plane, entire.

Plants dioecious. Androecia not seen. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem, the gynoecium base bulbous, fleshy, polystratose, and rhizoidous; bracts of innermost series much larger than leaves, erect and sheathing the perianth, the bracts deeply concave, broadly ovate to ± orbicular; apices with 4 short, lobes composed of ± regularly rectangular and (especially at the lobe extremities) irregularly sin-

uate-rhomboidal cells, the apical end of the marginal cells often diverging and forming a slight projection, the lobes thus crenulate; lamina composed of ± regularly subrectangular cells, those in distal sector rather thick-walled, those of remainder of bract (particularly the cells in a large median-basal field) thin-walled, the margin bordered by cells of variable shape and orientation, some hardly longer than wide, others ± sinuate-rhomboidal, the apical or free end of marginal cells variously divergent and forming a short projection or a tooth, the margin irregularly crenate-denticulate to the base, the teeth at most of 3 superposed cells; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth, the lobes composed of rather thick-walled, irregular, long, narrow, at times ± sinuate, papillose cells that at the apical end are laterally free for varying lengths, the lobes crenate-denticulate; perianth cells subrectangular below mouth, and here the cuticle is striate; perianth 2-stratose near base.

Sporophyte not seen.

DIFFERENTIATION—*Lepidozia glaucescens* differs from the other glaucous-leaved species of the genus by having distinctly asymmetrical leaves, with a ± straight dorsal margin (Fig. 39 : 1, 3, 4, 7). The leaf cells and the cortical cells of the stem (in surface view) are distinctly thick-walled (Fig. 39 : 11), rather than leptodermous as in *L. bisbifida* and *L. digitata,* and the wall thickenings have a distinctive lamellated (layered) appearance (Fig. 39 : 10). The first branch underleaf is typically undivided in both *L. glaucescens* and *L. glaucophylla.* The leaf insertion is narrow and varies from weakly to distinctly incubous, often on the same shoot.

The leaves of *L. glaucescens* are remarkable because of the unique combination of cells with discrete elliptical papillae and a ± uniform waxy, granular coating (Fig. 39 : 10). The papillae are hemispherical to short on the lobes (Fig. 39 : 10) but distinctly elongate in the median and basal sectors of the disc (Fig. 39 : 11). The waxy coating is poorly developed in many collections, however, and is often evident only on the new growth at the tips of the shoots. Consequently, *Lepidozia glaucescens* might be mistaken for *L. novae-zelandiae,* which also has a striate-papillose cuticle, similar leaf shape, and lobes terminating in a differentiated uniseriate row of elongated, thick-walled cells. Under the compound microscope, however, the leaf surface of *L. glaucescens* has a semiopaque, granular appearance, even if the waxy coating is not apparent under the dissecting microscope.

Plants with an apparent smooth cuticle but possessing ± flat discs with spreading lobes, ± straight dorsal margin of the leaf, and thick-walled lobe and disc cells, should be treated with great care. Some populations of the species have cuticlar papillae suboptimally developed; preferably, several leaves from various areas of several shoots should be examined (including leaves from near the shoot apex). Verification under oil immersion can be helpful at times.

DISTRIBUTION–ECOLOGY: Known only from Chatham Island and a few stations on South and North Islands, New Zealand.

Apparently a lower-elevation species; the South Island stations are all from between 120 and 300 m, while those from the North Island are from ca. 340–540 m. The type is from a damp forest, partially under log cover; the White Horse Creek specimens include a site beside a tarn in a pakihi area under manuka (*Leptospermum scoparium*; *Child H5436*) as well as boggy areas. In the southern portion of Westland (Monkey Puzzle Gorge), the species occurred in a very protected niche: over soil deep in a pocket under a mass of fallen trees in a forest dominated by *Nothofagus menziesii* and *Dacrydium.* Known from North Island only in the Waipoua Reserve area; the Engel collection from just north of Tutamoe is from a wet forest dominated by *Weinmannia silvicola,* occurring on the top of a bryophyte-covered log, while that from Te Matua Ngahere is from an *Agathis* forest with *Dacrydium* and other podocarps, with a strong understory of *Gahnia xanthocarpa,* where the species occurred in a shaded, protected niche on the ventral-lateral side of a log. The Schuster specimen is from a wet kauri forest. The Chatham Island plant is from damp rocks and banks in a dense broadleaf forest.

SELECTED SPECIMENS SEEN:—NEW ZEALAND. SOUTH ISLAND. WESTLAND PROV.: Monkey Puzzle Gorge, Cascade Road, Martyr River near Martyr Saddle, 120 m, *Engel 23042* (F); 1 km N of White Horse Creek, ca. 150 m, *Child H5416* as *L. glaucophylla* (F); 2 km N of White Horse Creek, ca. 150–300 m, *Child H5425, H5436,* both as *L. glaucophylla* (F). NORTH ISLAND. NORTH AUCKLAND PROV.: NE Waitakere Ranges, Spraggs Bush, NE end of Turanga Rd, ca. 340

m, *Braggins 99/298* (AKU); SE corner of Waipoua Forest, just N of Tutamoe, 540 m, *Engel 21087* (F); same loc., *Braggins 98/318* (AKU, f); Waipoua Forest, track to Te Matua Ngahere, ca. 340 m, *Engel 22572* (F); ibid., Big Tree Kauri area, near n–s road, *Schuster 67-3798* (F). CHATHAM IS.: Hattwoods Hole, Tuku a tamatea River, *Given* (F).

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Index to Taxa

Recognized taxa are in roman type and illegitimate or synonymous taxa are in *italics*. New taxa and new combinations are in **boldface**.